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Autecological-zoogeographical Analysis of Moss Mites (*Acari, Oribatei*) on the Basis of Fauna in the Poznań Environs. Part III

[Pp. 161—258]

Analiza autekologiczno-zoogeograficzna mechowców (*Acari, Oribatei*) na przykładzie fauny okolic Poznania. Część III

Автэколого-зоогеографичесский анализ панцирных клещей (*Acari, Oribatei*) на примере фауны окрестностей Познани. Част III

Abstract: The paper contains a zoogeographical analysis of the ranges of 177 moss mite species from the Poznań region. The following groups of species have been distinguished: European, Palaearctic, temperate-Holarctic, Holarctic, subbipolar, Holarctic-subtropical, temperate-Holarctic-tropical and semi-cosmopolitan. The paper is concerned with the percentage share of particular range groups in the composition of the moss mite fauna of the Poznań region, the interrelations between the ecological and geographical elements, the effect of humidity of the macroclimate on the distribution of the species under study, the dependence of the size of ranges of particular species upon their humidity requirements, and some problems of the historical zoogeography. On the basis of palaeontological materials and, above all, the structure of the present-day ranges an attempt was made to determine the period in which a given range was formed and, consequently, to establish the minimum absolute age of the species. Palaeogene, Neogene, and Quaternary species were distinguished. The postglacial history of the formation of the moss mite fauna in the Poznań region was also analysed. The species were classified in groups according to the time of their arrival in the study area. Probable changes that took place in the fauna in the Older and Younger Dryas and in the Subboreal and Subatlantic periods were also discussed.

CONTENTS

I. INTRODUCTION

The present publication contains a zoogeographical analysis of 177 species of moss mites based on factual material specified in the preceding parts (Rajski, 1967, 1968). Only three recent papers of essential importance (Hammer, 1966; Krivolutski , 1966a, b) and, in a few cases, certain unpublished data on

the occurrence of some species in North Vietnam have been included additionally.

I wish to express my sincere thanks to Prof. J. Rafalski and Dr. A. S. Kostrowicki for continued help which they lavished on me during my work at this paper. I am also grateful do Dr. Andrzej Szeptycki for his critical reading of the typescript.

The fauna of moss mites is poorly known as yet and there are still vast areas in Asia, Australia, Africa and both Americas from which we have no material at our disposal. Nevertheless, the number of publications on the distribution of moss mites throughout the world has recently increased, mainly thanks to the initiative of J. Balogh and M. Hammer as well as other investigators. Central Europe has always been one of the best-known regions in this respect, and in the latest period of some dozen years much valuable information about the distribution of moss mites in European Russia and Spain has been obtained, which altogether provides a fairly satisfactory, though still incomplete, picture of the moss mite fauna in Europe.

This state of matter induced me to undertake a zoogeographical analysis of the moss mite fauna of the Poznań region. Strenzke (1952) was the first to recapitulate the faunistic data on moss mites inhabiting Central Europe. However, he did not pay enough attention to the territory of the U.S.S.R. and, having in mind the fragmentary state of the faunistic material of that time, he did not even try to treat the informative material that he had collected in a synthetic manner. None-the-less, his work has proved very helpful in the present considerations.

The procedure based on the assignation of particular species to faunal provinces (or other units), i.e., defining them as the so-called faunal elements, has been given up and replaced by the adoption of contemporary ranges of moss mites as the basis of geographical division. In the course of investigation, various present-day systems of zoogeographical regionalization appeared to be ill fitted for use in detailed studies of moss mites. On the other hand, the present state of knowledge of the distribution of moss mites still leaves much to be desired, even in Europe, and consequently one should not carry their zoogeographical division too far.

Having taken the foregoing into account, I defined the ranges individually according to the method of Meusel et al. (1965) (full technical details will be found in the work by Meusel et al. 1965) by establishing their relation to the horizontal and vertical zonations and to the humidity of climate. The second part of the definition of a range offers the abbreviations of the geographical units in which the given species occurs. Such definitions were used as a basis for the combination of particular species of similar ranges into groups. A purely geographical sense is ascribed to these groups, and in their notion they approximate most closely to the „Geoelement" of Walter (1954). Some features of the ranges (disjunctions, Tertiary flora and fauna refuges) are given in separate columns to bring them out in full relief.

Distinction of genetic elements has been given up for lack of adequate data, but care has been taken in each case to determine very accurately what ecological element is represented by a given species. The relation to the plant cover and humidity have mainly been taken into consideration.

All these data (including the reports on fossil moss mites) were used to distinguish historical elements and chronoelements in the material examined. The historical element is formed by a group of species which joined a fauna (in the present case the fauna of the Poznań region) at the same time (Vul'f, 1943). The chronoelement is a group of species which came into being at more or less the same time (Walter, 1954).

It is obvious that in moss mites the distinction of historical elements and chronoelements is, for lack of fossil material, hypothetic in nature. However, since there is little hope for the obtainment of more abundant palaeontological material in the future, this is the only, though merely partial, way to reconstruct the history of the moss mite fauna.

This type of study has been initiated by Marie Hammer (1965) in her interesting work in which she tries to determine the approximate age of *Mucronothrus nasalis* (Willmann) on the basis of its present range. The minimum age of this species lies within limits of 58 milion and 140 milion years and, thus, it supports the generally accepted opinion that moss mites are a very old group. Inference concerning the history and age of a species or a higher taxonomic unit from its present range is nothing new, to be sure (Bartenef, 1934; Dansereau, 1957; Hormuzaki, 1930; Kryzhanovskiĭ, 1965; Pop, 1964; Szafer, 1964; Walter, 1954; Warnecke, 1958; Vul'f, 1944), and it has often been used to good effect. The inference from indirect premises is, besides, well established in the history of the development of human thought, and the historical geography of moss mites does not seem to be an exception as regards the possibilities of application of this method.

The wide ranges of numerous moss mite species are, in all probability, associated with the antiquity of this group. (Apart from this, I am not an adherent of the theory of direct correlation between the age and the range of a species. J. C. Willis, Age and Area, London, 1922). Old age and extensive range are, besides, distinctive characters of the whole soil fauna (Kühnelt, 1961).

The adoption of the proposition about the invariability of ecological demands of a species during the whole period of its existence seems to be essential for further considerations, for it allows the supposition that in the geological past the species dwelt for the most part in the same environments as they inhabit today. The conclusion based on this reasoning may, however, be charged with an error, because we do not know to what degree the present range is in accord with the ecological value of the species.

The problem whether the passive expansion of moss mites is possible is also important to the final conclusions, as it might explain both the large size of their ranges and the huge disjunctions, often existing in these ranges.

There are practically no moss mites in aerial plankton, as has been shown by its examination (for literature see SEYD, 1962); now only KRIVOLUTSKIĬ (1966a) supports the theory about easy passive movements of these species over vast areas, but he has not carried out any studies in this respect.

The above-mentioned inaccuracies certainly lower the value of the results to some extent, but they are in no relation to the actual achievements.

The following symbols and abbreviations will be used in this paper:

a — southern temperate zone
Afr — Africa
afr — African
Al — Alaska
Alg — Algeria
alp — Alpine
Am — North America
am — North American
and — Andine
ant — antarctic, Antarctic Province (south frigid zone)
arct — arctic, Arctic Province (north frigid zone)
Arm — Armenia
As — Asia
as — Asiatic
ast — southern subtropical zone
atl — Atlantic
b — boreal, boreal zone
bst — northern subtropical zone
C — central (in geographical sense)
Cap — Capensis
cap — Cape (used as adjective)
cf — coniferous forests
Col — Colchis
Cors — Corsica
df — deciduous forest of temperate zone
E — East
EAm — eastern North America
Eg — Egypt
eu — eury-
euh — euryhygr
Eur — Europe
eur — European
f — forest, silvan
Flor — Florida
Gr — Greenland
Haw — Hawaiian Is.
heur — holo-European
hhol — holo-Holarctic
Him — Himalaya Mts.
hol — Holarctic
hs — habitat of mosses and lichens on hard substratum
II — Ionian Is.
k_1 — continental climate zone
Kur — Kuril Is.
Len — Lenkoran Lowlands
m — meridional
Mad — Madeira
mad — Madeiran
man — Manchurian
MAs — Middle Asia
mas — Middle Asiatic
meso — middle portion of scale range
Mex — Mexico
mh — mesohygr
mo — montane level
moh — mesooligohygr
Mong — Mongolia
Mor — Morocco
mpeuh — mesopolyeuryhygr
mph — mesopolyhygr
msth — mesostenohygr
N — North
n — neutral
NAm — northern part of North America
ncl — non-classified
niv — nival tier
NZeal — New Zealand
o — oligo (lower portion of scale range)
oc_1 — oceanic climate zone
oc_2 — suboceanic climate zone
oc_3 — subcontinental climate zone
oh — oligohygr
omh — oligomesohygr
op — open (non-forest) areas
p — poly (upper portion of scale range)
pac — Pacific
pal — Palaearctic
peuh — polyeuryhygr
ph — polyhygr

pmeuh	— polymesoeuryhygr	sm	— submeridional (also submeridional zone)
pmh	— polymesohygr	smo	— submontane level
Pol	— Polynesia	Sph	— Sphagnum
pst	— polystenohygr	T	— remnants of Tertiary (Turgay) forests in Tashkent region
S	— South	temp	— temperate (also temperate zone)
salp	— subalpine zone	trop	— tropical (also tropical zone)
SAm	— South America	W	— West
sbip	— subbipolar	WAm	— western North America
sbt	— subtropical		
semi-cosm	— semi-cosmopolitan		
Sib	— Siberia		
sib	— Siberian		

II. ZOOGEOGRAPHICAL ANALISIS

A. Detailed Analysis

The following groups of species with similar ranges have been distinguished in the material under study: European species (34·94%), Palaearctic species (18·08%), Holarctic species (35·59%), and those widely distributed (11·57%).

1. European Species

The species confined in occurrence to the European territory may, in turn, be divided, as follows: holo-European (7·81%), West European (7·35%), Central European (7·35%), South European (6·22%), East European (2·82%), South-East European (2·26%) and North European species (1·13%).

a. Holo-European Species

This group consists of 14 species (Table I), which occur throughout Europe and represent the oceanic-suboceanic-subcontinental bioclimatic type.

Four of them are meridional-submeridional-temperate-boreal species and the remaining ones present the submeridional-temperate-boreal type. The ranges of most of these species are continuous. (Continuity or discontinuity of ranges is naturally a relative matter. In this paper a range is regarded as continuous, if between its particular localities there are no geographical barriers which might prevent contact between the populations living on both their sides).

Two of them show a South European-North African disjunction and one a European-Madeiran disjunction. Five species of this group occur in Colchis and the Lenkoran Lowlands. Some of them (underlined in Table I) are relict species. (For details see Section B. 5.). Six holo-European species occur in the mountains of the temperate bioclimatic zone, but only two of them reach as high as the alpine tier. Out of the remaining species, three were found in the subalpine zone and one in the montane.

Ecologically, they are mostly (9) species with medium and high humidity

requirements and inhabit the European deciduous forest zone. *A. pilosus* (C. L. Koch) (73) deviates considerably from this group in its ecological requirements; it occurs exclusively in very wet open areas (except for peat bogs). *L. licnophorus* (Michael) (114), though present in forests, has distinctly lower humidity requirements than other species and therefore it may be a more southern form. Two species live in mosses and lichens on a hard substratum and they, too, reveal a remarkably greater tolerance to low humidity than the forest species.

b. West European Species

This group embraces 13 species (Table II) which occur in Europe and represent the oceanic-suboceanic bioclimatic type or only slightly encroach on the subcontinental bioclimatic zone (mainly in the Bulgarian mountains).

The submeridional-temperate (5 species) and temperate (4 species) types predominate among the West European species. Besides, there are 2 meridional-submeridional-temperate-boreal species and 2 submeridional-temperate-boreal ones. They all have continuous ranges except for *X. permixtus* (André) (72). The eastern boundary of distribution of nine species of this group runs in Poland (Table II, indicated by „+"), two of these species having their easternmost localities in the territory of Poland (Table II, indicated by „o"). In addition, nine species have their northern boundaries of distribution running across Poland and three of them occur here also in their northernmost localities. So far, only two West European species have been observed in the mountains of the temperate bioclimatic zone, and what is more, in the alpine tier. *X. permixtus* (André) (72) holds an exceptional position in this group, for it occurs in detached localities in the relict Tertiary (Turgay) forests near Tashkent (Krivolutskiĭ, 1966b), in the subcontinental climate and, probably also as a relict on Madeira.

This group is fairly well differentiated in ecological respect. Four species are forms of the Europen deciduous forest zone with medium or great humidity requirements. Two others, being mesohygric, also show some association with forests. As many as four species live in mosses and lichens on a hard substratum. They are probably at least mesohygric, as indicated by their dependence on macroclimate. The humidity requirements of only two of them have been determined hitherto. Three non-silvan species, of which one usually dwells in *Sphagnum*, show great humidity requirements. No oligohygric species occur in this group.

c. Central European Species

This group is composed of 13 species (Table III), which in Europe appear only in the subceanic climate zone or have a centre of occurrence in this zone and only slightly encroach on the oceanic or subcontinental climate zones.

The temperate bioclimatic type prevails among the Central European species (7 species). The other types represented are the temperate-boreal (2 species), the submeridional-temperate (3 species) and the submeridional-temperate-boreal (3 species). All these species have continuous ranges. Five

of the Central European species have their western boundaries of range running across Poland (one of them also the westernmost locality of its range), nine of the species have the eastern boundaries (five of them also the easternmost localities), five the southern boundary (one the southernmost locality), and six the northern boundaries (one the northernmost portion of the range) in the Polish territory. One species occurs in the mountains, but only in the subalpine zone.

The dominant species of the Central European group are those of deciduous forests (5 species), with medium and great humidity requirements. Besides, this group includes three polyhygric species found in peat, 2 species inhabiting mosses and lichens on a hard substratum, and a mesohygric species independent of plant cover. There are no xerophilous species.

No fewer than 3 species of this group are represented exclusively by single subspecies. The Central European species might be regarded as endemic in the fauna examined. Their small number gives evidence of the young age of the fauna of this region.

d. South European Species

This group is made up of 11 species (Table IV), which live in Europe and do not go beyond the northern boundary of the temperate bioclimatic zone (Meusel et al., 1965); they are all species of the oceanic-suboceanic-subcontinental type.

Nearly half of them (5 species) occur in the meridional, submeridional and temperate zones. The ranges of 4 species are discontinuous (South European-North African and European-Madeiran disjunctions). Some localities of these species in the meridional zone, situated in the oceanic climate region, are probably relict in character (Table IV, in black type). The other species, 6 in number, are of the submeridional-temperate type. The ranges of all these species are continuous and their northern boundaries extend through Poland, six of them having their northernmost localities in this country. Four species inhabit the mountains of the temperate zone: two the alpine tier, one the subalpine, and one the montane.

The South European species are chiefly characteristic of deciduous forests and have medium and, rarely, great humidity requirements. Only one species lives in mosses and lichens on a hard substratum, and the ecological requirements of two other forms are not clear.

e. East European Species

Five species (Table V), occurring or finding the best conditions for development in the suboceanic and subcontinental climate zones of Europe, belong to this group. Three of them have single localities in the oceanic climate zone.

Climatically the East European species are well differentiated. One of them represents the meridional-submeridional-temperate-boreal type. Its only locality in the meridional zone (Lenkoran Lowlands) is relict in character. Two species are of the submeridional-temperate-boreal type, one represents the

temperate-boreal type, and one the meridional-temperate. The range of this last species must be regarded as discontinuous, because the probably relict locality in the Lenkoran Lowlands is separated from the remaining localities by the whole submeridional zone. The other species have continuous ranges. Only one East European species has its westernmost locality and the northern and southern boundaries in Poland. Most of the ranges of the remaining species reach farther to the west, entering into the German territory. Two species inhabit the mountains of the temperate zone, one the subalpine tier and the other the alpine.

Only one East European species is definitely associated with open areas (meadows and fescue-wormwood steppes). One species is independent of plant cover and the other ones are forest forms with medium humidity requirements.

f. South-East European Species

This group consists of four species (Table V), whose centres of occurrence lie in south-eastern Europe.

The meridional-submeridional-temperate type is represented here by two species, and the submeridional-temperate and submeridional-temperate-boreal types by one species each. With respect to macroclimate they are differentiated into the oceanic-continental (1 species) and suboceanic-subcontinental types. Three species of this group have the northern boundary of their ranges in Poland. None of them has been found in the mountains.

As regards ecology, they are eury- and oligomesohygric species which occur most abundantly in the steppes of south-eastern Europe or even in semi-deserts, whereas in Central Europe they appear rarely and in small numbers. *A. polonicus* KULCZYŃSKI (66) is an exception in this group, since, being associated with deciduous forests, it has only relict localities amidst exuberant subtropical vegetation in the meridional and submeridional zones. Its range is discontinuous. On the one hand, it has been recorded from Poland, on the other hand, it has been found on the coast of the Black Sea, in Colchis and the Lenkoran Lowlands.

g. North European Species

This group is made up of only 2 species (Table V), which reach the greatest abundance in the boreal zone of northern or northern and eastern Europe.

One of them is a suboceanic and temperate-boreal species and the other is a suboceanic-subcontinental and submeridional-temperate-boreal-arctic one. The ranges of these species may be regarded as continuous. *P. tardus* FORSSLUND (14) has its southernmost locality in the territory of Poland and *C. subarcticus* TRÄGÅRDH (84) lives mainly in cold environments (mountains and peats) in Central and South Europe.

They both belong to the fauna of coniferous forests and have a high ecological value in relation to humidity.

2. Palaearctic Species

The species that live both in Europe and in Asia may be divided into the following groups: the European-West Siberian species (12·43 %), the European-Manchurian species (3·96 %), the European-Siberian species (1·13 %), and the European-Middle Asiatic ones (0·56 %).

a. European-West Siberian Species

This relatively numerous group (22 species — Table VI) includes forms dwelling in Europe and Western Siberia and reaching as far as Central Mongolia.

Two bioclimatic types predominate among them, the meridional-submeridional-temperate-boreal (7 species) and the submeridional-temperate-boreal (8 species). The other types represented in the material are the submeiidional-temperate (3 species), temperate-boreal (2 species), temperate and submeridional-temperate-boreal-arctic (1 species either). The oceanic-suboceanic-subcontinental forms prevail in all these categoiies, but there are some deviations towards a greater tolerance to the continental climate and a smaller tolerance to the oceanic. D. (H.) riparius (NICOLET) (49), O. neerlandica (OUDEMANS) (94) and *E. tardus* (C. L. KOCH) (120) make up a southern element and *A. tragardhi* FORSSLUND (104) a northern element of the European-West Siberian group of species.

A disjunction which extends approximately from the Kuznetsk Ala-Tau to Europe oi, in a smaller number of cases, from Central Mongolia to Europe, is a distinctive feature of this group. In addition, three species have a South European-North African disjunction. Four species seem to have relict localities in the Lenkoran Lowlands, Colchis and Tashkent region.

Precisely half the European-West Siberian species live in the mountains of the temperate zone, two of them in the nival tier, six in the alpine tier, two in the subalpine and one in the montane. *T. trimaculatus* (C. L. KOCH) (138), dwelling in the nival tier in the mountains, is at the same time the only member of this group occurring also in the Arctic Region.

Ecologically, the European-West Siberian species are fairly well differentiated, but most of them are meso- or mesopolyhygric. Only three species have small humidity requirements. The relation of the species to the plant cover is as follows: nine of them are forest form, three independent of plant cover and five are meadow forms, out of which four have also been found in steppes. They tolerate salinity and tillage. Three species occur in mosses and lichens on a hard substratum. Of these, *T. trimaculatus* (C. L. KOCH) (138) is also fairly numerous in steppes.

b. European-Manchurian Species

These species (Table VII), seven in number, live in Europe and eastern Asia especially in Japan. Two of them occur, besides, in northern Africa and two in western Siberia.

They represent the following bioclimatic types: meridional-submeridional-temperate-boreal (3 species), submeridional-temperate-boreal (2 species), sub-

meridional-temperate (1 species) and temperate (1 species). All of them are oceanic-suboceanic-subcontinental species. *C. pusillus* (Berlese) (148) is a southern form in this area.

A typical disjunction of this group is the European-Manchurian one. Only two species have intermediate localities in western Siberia. Three species show also a South European-North African disjunction or a European-Madeiran one. *X. clypeator* Robineau-Desvoidy (71) occurs in a presumably relict locality in the remains of the Tertiary (Turgay) forests in the Tashkent region.

Only *C. falcata* Evans (74), representing the temperate type, has not been found in mountains hitherto. The other species appear in the alpine (3 species), subalpine (2 species), and at least montane (1 species) tiers in the temperate zone.

The European-Manchurian species are for the most part forest forms, and three of them show a clear association with deciduous forests. Only one species, which has low humidity requirements, occurs in mosses and lichens on a hard substratum and is also fairly abundant in the steppes of south-eastern Europe.

The number of the European-Manchurian species in the fauna under study is small and forms somewhat less than 4%, whereas Kostrowicki (1965b) writes that their number fluctuates from 10 to 15% in particular European and East Asiatic faunas. In fact, this figure for the fauna of moss mites of the Poznań region seems to be larger, but as the knowledge of Asiatic moss mites is still poor, not all of them have been detected so far.

c. European-Siberian Species

Only two species (Table VII) of the European-Siberian group have been found in the Poznań region. They are both submeridional-temperate-boreal and oceanic-continental species. Their ranges are probably continuous. In the mountains of the temperate bioclimatic zone these species reach the alpine tier. One of them is a forest form and has small humidity requirements, the other inhabits meadows as well as steppes and is a polymesohygr.

d. European-Middle Asiatic Species

In this group I include one species (Table VII) living in Europe and Middle Asia. It represents the meridional-submeridional-temperate-boreal and oceanic-continental types. In Asia it is fairly abundant in the area of semi-deserts to the east of the Aral Sea. In Europe, single specimens were encountered in peat-bogs and in dry places exposed to the sun's rays. It tolerates salinity.

3. Temperate-Holarctic Species

These species inhabit Eurasia and North America with the exception of the Arctic Province and they may be divided, in general, into the temperate-holo-Holarctic species (8·46%), the western temperate-Holarctic species (10·68%), and the alpine temperate-Holarctic species (0·56%).

a. Temperate-Holo-Holarctic Species

This group is composed of 15 species (Table VIII) living in Europe, Asia and, in most cases, in eastern North America. In addition, some of them occur in northern North America, in its western part or in northern Africa.

More than half the species are of the meridional-submeridional-temperate-boreal bioclimatic type (9 species). The submeridional-temperate-boreal species are less numerous, 5 in number, there being one submeridional-temperate species. With the exception of four species of the first group which are of the oceanic-continental type, all the members of this group represent the oceanic-suboceanic-subcontinental type. *M. minima* (BERLESE) (18) is a southern form of this group.

A distinctive character of the ranges of these species is their North Atlantic disjunction and, in some cases, European-Manchurian, North Pacific, North American, and South European-North African disjunctions. All the species of this group inhabit territories in which the Tertiary flora and fauna may have lasted out, but only the localities of two species (Table VIII — in black type) in Colchis and Lenkoran Lowlands are probably relict ones.

Most of the holo-Holarctic species (except two) appear in the mountains of the temperate bioclimatic zone: five in the alpine tier, four in the subalpine, and two in the montane.

The ecological differentiation is not great as for species with so extensive ranges, but they have a relatively high ecological value. Forest species with medium or great humidity requirements predominate in Central Europe. Some of them are, however, fairly numerous in meadows and even in steppes (5 species) and semi-deserts of the Middle Asiatic zone of continental climate (Table VIII). It is interesting that *O. subpectinata* (OUDEMANS) (99) occurs both in peats and in steppes. Two species are true peat-inhabitants: *N. coronata* BERLESE (41) and *P. tenuiclava* (BERLESE) (159).

b. Western Temperate-Holarctic Species

This is a comparatively numerous group (Table IX — 19 species) composed of forms that live in Europe and eastern North America. Some of them are also known from North Africa, Madeira, and western North America. However, they have not, as yet, been recorded from Asia.

The bulk of the western Holarctic species represents two bioclimatic types, the meridional-submeridional-temperate-boreal (7 species) and the submeridional-temperate-boreal (9 species). The oceanic-suboceanic-subcontinental type predominates, but there are some instances of reduced tolerance to the oceanic (2 species) or the cubsontinental (1 species) climate. *N. elegantula* (BERLESE) (42) and *C. mediocre* BERLESE (133) are southern forms and *S. areolatus* BERLESE (77) is a northern species of the group under discussion (Table IX).

The ranges of the western Holarctic species are marked by a North Atlantic disjunction and, in some species, South European-North African, European-Madeiran, and, in two species, North American disjunctions. All the species of this group occur in refuges of the Tertiary forest fauna and flora, six species having, besides, their probable relict localities in this territory (Table IX — in black type).

Somewhat more than half the western temperate-Holarctic species live in

the mountains of the temperate bioclimatic zone: ten in the alpine tier, three in the subalpine, and one in the montane.

Ecologically, the forest species with medium and great humidity requirements prevail also in this group, but there are, in addition, a few forest mesooligohygric species and even one with decidedly small humidity requirements. *A. ovatus* (C. L. KOCH) (70), being a forest form, occurs also in the South-East European steppes. Out of the remaining species, three show a great independence on plant cover, as they dwell both in forests and in meadows. Further three species reveal clear preference for open areas, *T. novus* (SELLNICK) (140) occurring also in steppes.

c. Alpine Temperate-Holarctic Species

In the material under study I found only one species inhabiting all ever the temperate (s. l.) part of the Holarctic and reaching its peak of abundance at great altitudes, whereas in lowlands it occurs almost exclusively in cold environments of high humidity (peat-bogs) and even then in small numbers (Table VIII).

It is an alpine submeridional-temperate and oceanic-suboceanic-subcontinental species, also very numerous in the nival tier. Its range shows a Euro-Asiatic disjunction, which stretches throughout south-western Siberia, and a North Atlantic disjunction.

4. Holarctic Species

These species are more or less widely distributed all over the Holarctic Province including the Arctic. They can be classified in 3 groups: holo-Holarctic species (10·17 %), western Holarctic species (5·09 %) and alpine Holarctic species (0·56 %).

a. Holo-Holarctic Species

This is a group of 18 species (Table X) occurring in Europe, Asia, and North America in the temperate zone (s. l.) as well as in the Arctic Province. They generally cross the Arctic Circle in Greenland, North Canada, and, in some cases, also on the islands of the Arctic Ocean.

They include two bioclimatic types: the meridional-submeridional-temperate-boreal-arctic (10 species) and the submeridional-temperate-boreal-arctic (7 species). The oceanic-suboceanic-subcontinental forms predominate in both these types. Only four species tolerate also the continental climate. *H. paolianus longisetosus* WILLMANN (30) and *O. translamellata* (WILLMANN) (100) are northern forms in this area.

All these species have their ranges disrupted, often repeatedly, but there is not a disjunction characteristic of all the forms. The disjunction between Europe, Greenland and North Canada is the commonest. Besides, there are North Atlantic, North Pacific (between Japan and Alaska), South European-North African, and European-Manchurian disjunctions. In the case of this last disjunction there is often an intermediate locality in the Kuznetsk Ala-Tau region. All the species of this group occur in the refuges of the Tertiary flora

and fauna, but only several such localities (Table X — in black type) may be relict in character.

Most of the holo-Holarctic species inhabit the mountains of the temperate bioclimatic zone, 11 in the alpine tier and 2 in the subalpine. There is also a species living in the mountains of the meridional zone, probably in the alpine tier (Sikkim, Himalayas).

Most of the species discussed have a high ecological value and they generally constitute mixed types, namely, six species may be regarded as forest ones (these are both mesooligohygrs and mesopolyhygrs), five species show no dependence on the plant cover (two with low humidity requirements and as many as 3 polyhygric forms), two species have clear preference for open habitats (they are meso- and polyhygric), one is a peat-inhabitant, and three species with low humidity requirements are more or less distinctly associated with an extreme environment of mosses and lichens on a hard substratum. Except for the only peat-inhabitant each category contains species occurring also in steppes. These are nine altogether.

b. Western Holarctic Species

This is a group of 9 species (Table XI) living in Europe and North America and encroaching on the Arctic Province in Greenland and northern Canada. Some of them occur also in Africa or on Madeira, but they have not been recorded from Asia.

This group much resembles the holo-Holarctic species in bioclimatic respects. *T. foveolatus* WILLMANN (38) and *A. latitecta* (BERLESE) (126) are northern species. All the species of this group have discontinuous ranges, the commonest disjunction being that between Europe, Greenland and northern Canada, In addition, there are North Atlantic, South European-North African, and European-Madeiran disjunctions. Nearly all these species were observed in the refuges of the Tertiary flora and fauna, but probably only *P. punctata* (NICOLET) (123) has relict localities in Transcaucasia and on Madeira. Four species of this group occur in the alpine tier and one in the subalpine in the mountains of the temperate zone.

Unlike the holo-Holarctic species this group is fairly uniform ecologically: four species are associated with forests and four with open areas, two of the forest species occurring also in steppes. One species is a typical peat-inhabitant. There are no oligohygric species, and those with great humidity requirements are generally prevalent.

c. Alpine Holarctic Species

In the study material such a range is represented only by *C. horrida* (HERMANN) (26). It is a meridional-submeridional-temperate-boreal-arctic and oceanic-continental species. It occurs in fairly large numbers only in mountains up to the nival tier inclusive, where it multiplies intensely. In lowlands it dwells in mosses and lichens on a hard substratum. Its range shows North Atlantic, North Pacific (between Siberia and Alaska), and South European-North African disjunctions.

5. Subbipolar Species

The species of this group (Table XII) occur in the northern and southern hemispheres with a disjunction in the tropical and subtropical regions.

In the southern hemisphere they were observed only in the temperate zone. In the northern hemisphere their ranges are meridional-submeridional-temperate-boreal (2 species) and submeridional-temperate-boreal (1 species). Like most forms of the Poznań region they occur in the oceanic, suboceanic and subcontinental (2 species) zones and 1 species tolerates, in addition, the continental climate.

In addition to the typical disjunctions in the subtropical and tropical areas (Europe-Cape Province, North Africa-Cape Province, North America-South America), their ranges have a North Atlantic disjunction. All these species occur in the refuges of the Tertiary flora and fauna. In the mountains of the temperate bioclimatic zone one of them reaches the alpine tier and one the subalpine.

All the species have medium and high humidity requirements, are largely independent of plant cover (forests, open areas), and all occur in steppes. Only *G. elimata* (C. L. Koch) (156) evidently avoids forests, instead it occurs even in semi-deserts.

6. Holarctic-Subtropical Species

This group embraces 7 species (Table XII) which outside the Holarctic (Arctic Province inclusive) occur in the northern (2 species) and southern (4 species) subtropical areas or in both of them (1 species).

Besides the disjunction in the tropical zone (except 2 species), their ranges are also discontinuous within the Holarctic and they have North Atlantic (all species), European-Manchurian (4 species), South European-North African (3 species), and North American-South American (2 species) disjunctions. All these species occur in typical refuges of the Tertiary flora and fauna, but only one locality in the Lenkoran Lowlands may be regarded as a relict locality (Table XII). In the mountains of the temperate zone 3 species were noted in the alpine tier and 2 in the subalpine. The southern subtropical zone has also one species, *S. pallidulus* (C. L. Koch) (173), living in mountains (3800 m a.s.l. at 17° S and 1200 m a.s.l. at 25° S).

As far as ecology is concerned, the species which are independent of plant cover but associated with rather high humidity predominate (mesopolyeuryhygric species, 4 in number). The others are mesohygric species, one of which shows clear preference for open areas and the remaining two are forest forms. Five species, of which one is a forest species, occur also in steppes.

7. Temperate-Holarctic-Tropical Species

This small group consists of species widely distributed in the Holarctic (Arctic Province exclusive) and occurring in the tropical area and, in one case, also in the southern subtropical zone (Table XIII).

By the nature of things their ranges are disjoined in several places. The commonest is the North Atlantic disjunction, followed by the South European-North African and the North American-South American. *T. sarekensis* TRÄGÅRDH (87), which occurs in Europe, Greenland, and Hawaiian Is., holds a particular position. Presumably its true range will be established only in the future. All the temperate-Holarctic-tropical species can be found in refuges of the Tertiary flora and fauna.

Three of them were noted in the mountains of the temperate zone up to the subalpine (2 species) and alpine (1 species) tiers inclusive, two species were observed in the alpine tier in the tropical zone.

All the species present a high ecological value. As to their humidity demands, two of them are euryhygric and two are mesohygric. Three species are independent of plant cover (forest, meadow), one showing a distinct tendency towards open areas. Finally, one species is characteristic of mosses and lichens on a hard substratum. All of them were encountered in steppes.

8. Semi-cosmopolitan Species

These species of the fauna under study are distributed most extensively (Table XIII). They occur in the Holarctic (half of them, i.e., 3 species, with the exception of the Arctic Province). Besides, they can be found in the tropical and subtropical zones, in the southern temperate zone, and one of them even in the Antarctic Province. Their ranges vary in details so remarkably that it is impossible to give a general definition of the range for the whole group.

The ranges of these species are discontinuous, but there are no disjunctions characteristic of the whole group. The discontinuities found in them are European-Manchurian (in one case with an intermediate locality in Western Siberia), North Atlantic, South Pacific, North American-South American, North Pacific, and South European-North African disjunctions. All the species but one occur in typical refuges of the Tertiary flora in the northern hemisphere.

Half the species appear in the alpine tier of the mountains in the temperate zone and one, *H. initialis* (BERLESE) (168), at altitudes from 3000 to 3900 m a.s.l. in the tropical zone.

The species with medium humidity requirements and independent of plant cover predominate (3 species). Two species are peat-inhabitants and one dwells in large numbers in forests, being less numerous in different non-forest habitats including steppes.

B. General

1. Percentage Share of Species with Different Types of Ranges

Although practically each species has its own individual range, different from that of the other species, yet irrespective of details they may be combined in groups so as to facilitate the formation of a general opinion on the composition of the fauna. Such an analysis is presented in Table XIV.

The moss mite fauna of the Poznań region may be, in general, divided into five groups, in which, at a firet sight, the European species predominate decidedly (nearly 35%). So far as abundance is concerned, the temperate-Holarctic species come in second (nearly 20%) and are followed by the Palaearctic species (about 18%), the Holarctic species (nearly 16%) and those widely distributed (11·6%). The dominance of the European species is, however, factitious to a great extent, since on account of the fact that the Arctic Province belongs to the Holarctic (Kostrowicki, 1965b, and others) the temperate-Holarctic and Holarctic species should rightly be treated together and then they form more than 35% of the moss mite fauna of the Poznań region. The separate treatment of these species has been inspired not by the author's opinions on the problem of regionalization, but only by his desire to emphasize the principal difference between the range sizes of these groups. Thus, an essential character of the fauna under study seems to be the remarkable share of the widely distributed forms.

If the whole moss mite fauna of the Poznań region is taken into account, special emphasis is due to the relatively low share of the Central European species (Table XIV), which might possibly be regarded as endemic forms.

The clear advantage of the combined temperate-Holarctic and Holarctic species (about 35%) over the Palaearctic species (about 18%) is an interesting fact.

Out of the European group, the species distributed throughout Europe as well as the West European, Central European, and South European ones are represented in more or less equal proportions (6·22%—7·81% in particular groups). The share of the East and North European species is several times smaller (1·13%—2·82% in particular groups).

The European-West Siberian species predominate among the Palaearctic ones, which seems to be ecologically conditioned. Poor exploration of Asia in this respect accounts for the supposition that the proportional share of the particular range groups among the Palaearctic species will undergo a change. However, the generally small number of the Palaearctic species as well as that of their particular groups gives indirect evidence of the dominance of southern and western elements, which dominance is distinct among the European species. Hormuzaki (1930) described a similar situation for the butterfly fauna of Romania. In the fauna under study this phenomenon is less obvious among the temperate-Holarctic species (though even here the western tem-

perate-Holarctic element — 10·73% — preponderates over the temperate-holo-Holarctic — 8·48%) to disappear completely in the group of Holarctic species (Table XIV).

The alpine species form quite a small proportion of the fauna, which is only natural under lowland conditions specific of the Poznań region.

The above-mentioned dominance of the western and southern species in the fauna of this region can be observed also when we isolate the southern, northern or any other geographical element not only from the other European species, but also from all the range groups distinguished (Table XV). For about 29% of the species of the fauna examined the Wielkopolsko-Kujawska Lowlands lie in a sense on the border of their ranges and therefore one can speak of their eastern, western, or the like nature in relation to the study area. In the material arranged in this manner the southern species (10·16%) predominate and are followed by the western (7·35%), northern (4·52%), south-western and eastern (2·82% each) and alpine (1·12%) species. Though the contribution of particular groups has changed (increase in the proportions of southern and northern species), the general tendency is the same as in the European species, i.e., the southern and western species predominate.

Poor knowledge of the moss mite fauna in Asia may cause a change in these proportions in the future in so far as the Palaearctic and Holarctic species are concerned. On the other hand, Europe seems to have been examined well enough and so the regularity of this dominance of southern and western species over the remaining European species in the area of the Wielkopolsko-Kujawska Lowlands is certainly objective in character.

An analysis of the percentage composition of the moss mite fauna in the environs of Poznań allows the following generalizations:

The fauna under study is little specific, which is expressed by the dominance of widely distributed species and the small share of Central-European species. These facts are connected with the short period of formation of the fauna in the region of Poznań and with the nature of the European Lowlands, making the free passage of species along the east-west axis possible.

Among the species whose ranges are oriented in relation to the environs of Poznań the southern and western species prevail over the northern and eastern ones. This may indicate the origin of the fauna examined after the retreat of the glacier.

The small contribution of south-eastern species admits the supposition that the progressing process of changing of Wielkopolska into a more steppe-like region, has not as yet added in an essential way to the enrichment of the moss mite fauna of this area in steppe species.

2. Relations between Ecological and Geographical Elements

To begin with, I should like to emphasize, so as to avoid a misunderstanding, that I use the term „ecological element" exclusively to designate the requirements of species in relation to environment, expressed by their occurrence

in habitats characteristic of particular forms. Detailed characteristics of this kind are provided for all the species in appropriate columns of Tables I—XIII. It is not the purpose of this section to deal with the relation of an ecological element to the morphological-ecological types of moss mites (KRIVOLUTSKIĬ, 1965), life-forms (KLIMA, 1956), ecological types (BULANOVA-ZAKHVATKINA, 1952) and other similar notions which in contradistinction to the ecological element comprise also some morphological contents.

In the fauna examined I managed to distinguish 14 ecological elements (Table XVI), of which 6 were mixed (columns 2, 4, 7, 8, 10, 11, 13). Ten species (column 15) could not be classified in any of these elements, since their ecology was not sufficiently well known.

It may be stated, in general, that about 53% (the total in this case exceeds 100%, because the mixed elements can occur in both the basic groups) of the fauna examined (Table XVI, columns 1—7) shows association with forests and, as a result, belongs more or less clearly to the forest element. The second largest group (25·98%) is the meadow or meadow-steppe element (Table XVI, columns 2, 4, 7, 10, 13 and 14). The three other main elements, one independent of plant cover (12·99%), one xerophilous (9·04%) and one associated with peat-bogs (7·34%), are evidently less abundant.

The forest element is not uniform. The non-specific forest species, which form more than a quarter of the whole fauna (Table XVI, columns 1 and 2), prevail in it. Most of these species have large Holarctic (s.l.) ranges (28 in 48). A fairly large proportion of the species (10 in 48) show Palaearctic ranges, whereas considerably smaller numbers of them have European ranges and those larger than Holarctic (5 of each). Therefore, it may be generalized that the non-specific forest species of the moss mite fauna of the Poznań region belong, for the most part, to the Holarctic and Palaearctic elements and, consequently, have relatively large ranges.

The species of deciduous forests (Table XVI, columns 3 and 4), which form above 18% of the fauna examined, have generally smaller ranges. Only one species has a western temperate-Holarctic range, one a Europen-West Siberian range, and three of them have European-Manchurian ranges. The remaining species (28 in 33) have European ranges. Thus, the European range may be assumed to be typical of the species of deciduous forests in the moss mite fauna of the Poznań region.

The species of coniferous forests (Table XVI, columns 5 and 6) play a minor part in this region. Neither do they belong, as clearly as the groups discussed above, to a single geographical element. The species with Holarctic ranges predominate in this group (6 in 11), the remaining ones being distributed nearly equally between the European and Palaearctic elements (3 and 2 species, respectively).

The xerophilous element (Table XVI, column 7—10) consists of species living in mosses and lichens on a hard substratum. They are 16 in number, of which 7 have European ranges, Holarctic and Palaearctic ranges fall to

3 species each, and 1 species has a temperate-Holarctic-tropical range. The xerophilous moss mite species of the Poznań region therefore exhibit some advantage of the European element. It is striking that these species bear no relation (with two or three exceptions) to the Pontic transition zone (KOSTROWICKI, 1965b).

The bog-inhabiting species (Table XVI, column 11) have mostly Holarctic ranges (5 in 10). In the European element and among the widely distributed forms they are represented by fewer species (3 and 2, respectively). No bog-inhabiting species with a Palaearctic range have been found in the fauna under study. Thus, the species with wide (Holarctic and larger) ranges predominate among the bog-inhabitants. Three species that occur in peat-bogs as well as in open areas, not excepting steppes (Table XVI, column 10), need a separate discussion. South-east European *P. sellnicki* (WILLMANN) (143) and European-Middle Asiatic *P. hexagonus* (BERLESE) (142) were regarded as typical bog-inhabitants until quite lately. It has only recently turned out that they occur in considerably larger numbers in steppes (in the first case) or even in semi-deserts in Middle Asia (in the second case). They probably belong to the steppe-meadow element. On the other hand, Holarctic *O. subpectinata* (OUDEMANS) (99), though present also in Kazakhstan and Middle Asia, is more abundant in European peat-bogs. Thus, it still more augments the typical range group of bog-inhabitants in the fauna of the Poznań region, the Holarctic element Another problem is the detection of the factor limiting the occurrence of these species, which seems impossible at present

The species associated with open areas (Table XVI, columns 14, 2, 4, 7, 10, 13), or the ones which might be regardes as steppe-meadow species, should be analysed separately in two groups. In respect of their ranges some of the mixed forest-meadow elements (columns 2 and 4) are evidently inclined towards the forest one, prevailing appropriately in the groups of Holarctic and European species.

The typical steppe-meadow element (Table XVI, column 13) shows quite a unifoım distribution in all the four basic geographical elements distinguished. Perhaps its remaining mixed elements, especially the xerophilous meadow-steppe one (Table XVI, col. 9), should not be placed in the same category as the typical xerophilous element which represents above all the European range.

A distinctive character of the species independent of plant cover (Table XVI, col. 14) are their wide ranges. The widely distributed geographical element predominates evidently (out of the 23 species, 9 have ranges larger than Holarctic and 7 have Holarctic ranges).

To sum up the foregoing, it may be stated that the typical ecological element of the European geographical element in the fauna under study are the species of deciduous forests and the xerophilous species inhabiting mosses and lichens on a hard substratum.

A typical ecological element of the Holarctic element are the non-specific forest species, the species of coniferous forests and the bog-inhabitants.

A typical ecological element among the widely distributed species are the forms independent of plant cover.

The Holarctic element is the richest in ecological elements peculiar to it, the Palaearctic element is the poorest.

3. Relation of Moss Mite Fauna to Humidity of Macroclimate

The relation of particular forms to the humidity of macroclimate has been included in the definitions of the ranges, worked out after the formula given by Meusel et al. (1965). However, it seems that in order to explain some general regularities of this relation, the particular data mentioned above should be generalized. Table XVII isintended to serve this purpose. In it all the species occurring in the fauna examined are listed and arranged according to their ranges and the zones of humidity of the macroclimate. By a climatic type I still mean the relation of a particular species to the zones of humidity of the macroclimate marked out by Meusel et al. (1965). Thus, the species that occurs in all the four zones distinguished by this author (Table XVII, column 1) will be of the oceanic-suboceanic-subcontinental-continental type (abbreviated to $oc_{1-2-3}-k_1$), etc.

In the fauna examined I managed to distinguish 5 fundamental climatic types: oceanic-suboceanic-subcontinental-continental (12·43%), oceanic-suboceanic-subcontinental (69·49%), oceanic-suboceanic (6·78%), suboceanic-subcontinental (6·79%), and suboceanic (4·52%).

Dominant in the moss mite fauna of the Poznań region is the oceanic-suboceanic-subcontinental type and it predominates to such an extent that practically the whole fauna under study is oceanic-suboceanic-subcontinental in character. This is only natural because the boundary between the suboceanic and subcontinental zones runs in Byelorussia, just near the Polish frontier and the boundary between the oceanic and suboceanic zones extends across Mecklenburg, hardly getting clear of the north-western strip of Poland. The oceanic-suboceanic-subcontinental species are represented in all the geographical elements distinguished and predominate in the holo-European, South-European, European-West Siberian, European-Manchurian, temperate-holo-Holarctic, western temperate-Holarctic, holo-Holarctic and, less distinctly, in other elements. They are lacking in the ragne groups that were distinguished on the basis of occurrence of their species in one or two climatic zones only.

In respect of abundance the oceanic-suboceanic-subcontinental-continental types comes in second, though it is represented far less numerously. The continental climate zone is at a great distance from Poland and for this reason there are few of these species in our fauna. Except for the European element, in which this type practically does not occur, it is found in more or less uniform proportions in all the remaining elements: Palaearctic, Holarctic s.l., and relatively most abundantly among the widely distributed species. It pre-

dominates merely in the European-Siberian and European-Middle Asiatic elements, which, however, are composed of single species only.

The remaining types, oceanic-suboceanic, suboceanic-subcontinental, and suboceanic, form a slight proportion of the fauna examined (Table XVII, cols. 6—9), though they contain the very species that might provide evidence of the specific nature of the fauna of the Poznań region. This is especially true of the suboceanic type, represented worst, because Poland lies whole in the suboceanic bioclimatic zone.

In addition to the West-European element the oceanic-suboceanic species (Table XVII, cols. 3 and 6) occur also in the Holarctic s.l. They are missing among the Palaearctic forms and practically also among those widely distributed.

The suboceanic-subcontinental type is, above all, represented by the European species and, besides, it occurs in the European-West Siberian and western temperate-Holarctic elements.

Finally, the suboceanic type can be found exclusively among the European species.

A general conclusion made on the basis of the examination of the relation of climatic types to the ranges supports the generalizations set forth previously on the dominance of the widely distributed forms, in the case in point, those of the oceanic-suboceanic-subcontinental type, in the moss mite fauna of the Poznań region, and on the small share of forms specific of the study area or those of the suboceanic type.

4. Range Size and Humidity Requirements of Moss Mites

In 1962 in her paper on the Chilean moss mite fauna M. Hammer stated that the moss mite fauna of damp biotopes is more cosmopolitan in character than the xerophilous one. This phenomenon is due to the greater stability of ecological circumstances in the proximity of fresh-water reservoirs than in dry areas, which are dependent on periodical climatic changes to a markedly greater extent.

In the moss mite fauna of the Poznań region I have distinguished 4 groups of species with different humidity requirements: hydrophilous (Tables I—XIII, column: ecological element — pst, ph, pmh, pmeuh, peuh), those with moderate humidity requirements (msth, mh, mph, mpeuh, moh), xerophilous (oh, omh) and independent of humidity (euh). These groups have been divided according to particular geographical elements to which their species belong and characterized with absolute and relative figures in Table XVIII. The last group consists of species with so far undefined humidity requirements.

The data arranged in this manner make it possible to check the moss mite fauna of the Poznań region for the above-mentioned regularity observed by M. Hammer. It appears that the group of oligohygric species (xerophilous) occurring in the Poznań region actually lacks widely distributed species com-

pletely (the ones M. HAMMER had in mind). On the other hand, the relative numbers of hydrophilous species and those with moderate humidity requirements stand close to each other and form, respectively, 13·7 and 12·0% of the total of species in their category. Thus the probability of meeting with widely distributed species is not confined to the polyhygrs only, but also exists, more or less equally great, among the mesohygrs. The relative number of species independent of humidity is approximately twice as large among the widely distributed forms, which is quite natural. These very species have evidently the best chances to develop extensive ranges.

M. HAMMER'S regularity finds no support among the Holarctic species of the moss mite fauna of the Poznań region, since, as will be seen from Table XVIII, poly- and oligohygric species occur in nearly equal proportions (25·0% and 23·0%) in this group. The comparatively large share of oligohygrs in the group of Holarctic species is natural on account of the dryness of the arctic climate. Contrariwise, the relative numbers of meso- and euryhygrs are approximately by half smaller, being 11·0 and 12·5%, respectively.

The poly- and mesohygric species, however, predominate over the xerophilous ones in the temperate-Holarctic element only that here the centre of gravity evidently shifts on the species with moderate humidity requirements (26·0%), whereas the hydrophilous forms come in second (18·1%). The proportion of oligohygrs is far smaller indeed.

A decided predominance of xerophilous forms (38·5%) is observed among the Palaearctic species even if the polyhygrs (9·1%) and mesohygrs (20·0%) are treated jointly. Among the species with European ranges all these three groups occur in absolutely equal proportions.

M. HAMMER'S (1962) regularity proves true in the material from the Poznań region for widely distributed species (for which it has been set up) and for the temperate-Holarctic ones, as well as for the Holarctic species but only in the case when the species with moderate and high humidity requirements taken together are opposed to the oligohygrs. As for the Palaearctic forms, this rule does not come true, even in this last case.

In connection with the foregoing the regularity under discussion should be interpreted so that among the oligohygrs there are fewer species relatively widely distributed than among the meso- and polyhygrs together.

5. A Historical Approach to Some Characters of the Ranges

a. Introductory

The purpose of historical biogeography is, among other things, to reconstruct the process of formation of ranges in time and space (TOLMACHEV, 1962; KOSTROWICKI, 1965a). To carry out this task, biogeographers base themselves mainly on the analysis of the present-day ranges and in the palaeontological data try to find a confirmation of the results obtained in this way. Lack of such data most not stop the progress of investigations concerning the history

of formation of the ranges of living organisms, the more so since in many cases we are unlikely to find any of them at all. Moreover, the palaeontological data, even if available, often provide poor information on old geographical ranges. I venture the opinion that the contemporary historical geography of plants has become an extensive and autonomic branch of science only because in addition to the palaeontological methods it uses analyses of recent ranges of plants, carried out from the historical point of view (SZAFER, 1964). It should be added that many a time the present development of palaeogeography has allowed fairly true reconstructions, which are next corroborated by suitable palaeontological finds (TOLMACHEV, 1962).

The recent ranges of moss mites are so poorly known that an attempt to reconstruct their development seems abortive at present. However, the general outlines of the ranges of certain species which are already available for us permit the determination of some of their characters, such as are typical of many animals and plants and can be localized more or less exactly in the geological past. The time of formation of a range and thus, indirectly, the age of the species may be inferred from them, but it must be kept in mind that this method, for the first time applied for moss mites by M. HAMMER (1965), makes it possible to establish only the fact when a particular characteristic of the range arose; the species itself must have come into existence earlier, perhaps much earlier, but I will not hazard any conjectures in this respect.

The objective that I have been concerned with in this section is to determine the approximate minimum age (i.e., the age of the oldest range character that can be established in time) of some species, using the available palaeogeographic data (MARKOV et al., 1965; SINITSYN, 1962) as well as those provided by the historical geography of plants (KENDEIGH, 1961; NEISHTADT, 1957; SZAFER, 1964; WALTER, 1954; VUL'F, 1944) and animals (BARTENEF, 1934; HORMUZAKI, 1930; KRYZHANOVSKIĬ, 1965).

I have adopted, after the majority of contempoıary biologists, the view that the polytopic origin of species is a rarity, which plays only a minor part in the world of living organisms (TOLMACHEV, 1962). It also seems indispensable to lay strong stress on the fact of adoption of WEGENER'S theory as the basis for all these palaeogeographic considerations. The use of modern data concerning the ecology of particular species for historical deduction demands, in addition, the recognition of the uniformity of ecological requirements of species throughout the time of their existence. As such initial qualifications are almost generally accepted in modern biogeographical-historical studies, they will be adopted here without detailed argumentation.

The problem of parallelism in the distribution of plants and animals is somewhat more disputable. When in the course of researches of the recent fauna we are in a position to study the relation of animal species to a definite phytosociological association, we often find lack of close relations of this kind, even in the soil fauna. However, the authors who have studied this problem

in its wider aspect (Thiele, 1956; Rajski, 1961) claim that animals generally reveal connections with a definite type of vegetation, which usually represents a higher phytosociological unit (order, etc.). Hence I take it that there are no grounds to call into question the similar dependence in the past. Besides, with respect to the past we are concerned not with phytosociological units but with landscape-building formations. The probability of occurence of such species in them as show similar biocenotic relations at the present time is therefore still greater. This method has also been used by other authors (Vul'f, 1943; Warnecke, 1958, and others).

Much attention has lately been excited by the problem whether it is possible for the microfauna to be transported in a passive manner for great distances. As regards moss mites, this problem has been decided unambiguously (for literature see Seyd, 1962). According to the results obtained so far, the dispersal of moss mites on an intercontinental scale is hardly probable.

b. Species from the Palaeogene and Range Characters Generated in This Period

An analysis of the recent ranges provides no grounds to make conclusions on the history of their formation reaching back further than the Palaeogene (Bartenef, 1934; Szafer, 1964).

The Palaeogene covers the period from 70 to 26 million years ago. In this period the climate of the northern hemisphere was far milder and more homogeneous than it is now. It was not before the Oligocene that the period of cooling and differentiation of the climate began. There were four climatic zones in the early Palaeogene.

The temperate zone (with subtropical elements) included the present-day North-American continent with Greenland, from the northernmost point to about 49° N in the west and 37° N in the east, and eastern Siberia. There was a land bridge between Asia and North America in the region of Bering Strait, north of it and perhaps also farther to the south. This area was occupied by arctic Tertiary forests, originally indistinctly differentiated into two parts, boreal and temperate with subtropical elements. They were made up of both deciduous and coniferous trees.

The subtropical zone embraced a relatively narrow ecotone along the southern boundary of the arctic Tertiary vegetation in North America, without reaching the present Atlantic coast. In Eurasia it extended as a broad zone from Korea, Japan, and Sakhalin through Asia and Europe up to the Scandinavian Peninsula and the British Isles. It was covered by thermophilous mixed coniferous-deciduous forests with subtropical elements.

As early as that time, the tropical zone was evidently tripartite. In North America it included the southern part of the U.S. and Mexico, in Eurasia the Indo-Malay area and nearly whole Central and North Europe, and in Africa its northern part.

Lastly, a warm and dry climate with savanna-like vegetation prevailed in a large part of Middle Asia, Central Asia, Arabia, probably also in a considerable part of Africa and in the central portion of Mexico.

The following changes had taken place in the arrangement of the zones by the end of the Oligocene.

In North America the boundaries of the zones shifted farther to the south and the arctic Tertiary flora differentiated clearly into a boreal part, void of thermophilous elements, and a temperate part, better developed in the east of the continent. The shift of the tropical zone towards the south occurred also in Europe and, as a result, the temperate zone covered both eastern and western Siberia and, as previously, northern Europe. The southern boundary of the temperate zone in Europe was moved somewhat southwards. The so-called Turgay flora developed in the temperate zone. It comprised deciduous and coniferous trees, of which the latter became predominant in eastern Siberia.

The temperate-subtropical transition area in Eurasia split into an East-Asiatic part (southern Kamchatka, Sakhalin, Japan, Korea, and the so-called Far East) and a European part. These territories were separated by a warm and dry climatic zone including Central and Middle Asia and Arabia. Loose scrubs amidst grassland formed the dominant type of vegetation of this region.

In south-eastern Asia the boundary of the subtropical zone was shifted rather markedly to the north. The so-called Poltava flora prevailed here. The boundary between the zone of dominance of the Poltava and Turgay floras ran from the north of England through Central Germany, the northern Ukraine, the southern Ural, central Kazakhstan, the region of Zaysan Lake and that of Pekin (Kendeigh, 1961; Sinitsyn, 1962; Vul'f, 1944). The arctic zone and those of tundra and taiga did not yet exist in the Palaeogene.

Against the background of these facts I should like to consider all the data that permit the inference on the Palaeogene age of some moss mite species or admit the possibility of formation of at least a part of a given range in the Palaeogene.

There is, above all, a direct evidence for the existence of 15 moss mite species of those living in the Poznań region now at the end of the Eocene and the beginning of the Oligocene. They were found in Baltic amber and examined by Sellnick (1919, 1931). According to the data given by many authors (Hammer, 1965; Hormuzaki, 1930; Kryzhanovskiĭ, 1965; Papp, 1959; Szafer, 1964), in the Eocene and Oligocene there were suitable conditions for the formation of amber in the forests situated on the border between the subtropical and tropical zones in Sambia in the Mazury Lake District. As amber was formed in the humid subtropical-tropical climate, the occurrence of the species found in it in the recent tropical or subtropical zone or at least in refuges in which tropical species may have preserved provides additional evidence of their old age (Szafer, 1964). These are the species mentioned by Sellnick (1919, 1931) among other moss mites from Baltic amber: *C. horrida* (Hermann) (26) — Table XI, *T. tectorum* (Berlese) (32) — T. X, *C. latus* C. L. Koch (57) — T. VIII, *E. oblongus* (C. L. Koch) (64) — T. II, *C. bipilis* (Hermann) (68) — T. XII, *X. clypeator* Robineau-Desvoidy (71) — T. VII, *C. coriaceus* C. L. Koch (76) — T. IX, *C. labyrinthicus* (Michael) (80) — T. XI,

O. minus (PAOLI) (93) — T. VIII, *A. longilamellata* (MICHAEL) (103) — T. VIII, *E. acromios* (HERMANN) (115) — T. VI, *O. meridionalis* BERLESE (128) — T. IV, *C. cuspidatus* (MICHAEL) (146) — T. XI, *E. rauschenensis* (SELLNICK) (164) — T. III, *L. similis* (MICHAEL) (169) — T. X.

Out of these species, only *C. bipilis* (HERMANN) (68) has been noted in the subtropical zone and even this only recently (Table XII). However, as the moss mites of the countries situated in the subtropical and tropical zones are very poorly known, it may be supposed that most of the remaining species from amber also occur in them. Four of the species mentioned, *C. bipilis* (HERMANN) (68), *X. clypeator* ROBINEAU-DESVOIDY (71), *O. minus* (PAOLI) (93), and *C. cuspidatus* (MICHAEL) (146), live in refuges in which some Palaeogene elements may have been preserved (VUL'F, 1944), namely on Madeira, in Colchis and in the Lenkoran Lowlands. The species recorded from amber have very various ranges, from small West- and Central-European ranges to Holarctic-subtropical ones. No regularity can be detected here. The fact of finding recent moss mite species in amber is not only significant as direct evidence of their Early-Tertiary age. Its basic import consists in proving that this group of animals was able to survive such a long space of time keeping its specific characters. An intense speciation took place in most of the other animal groups, especially among insects, during that time (HORMUZAKI, 1930; KRYZHANOVSKIĬ, 1965).

The periods of formation of the ranges of the remaining species may be referred to the Palaeogene only indirectly, by comparing the distinctive characters of their ranges with the palaeogeographic and palaeobotanic data.

(1) In SZAFER'S opinion (1964, p. 256), the main refuge of the Early-Tertiary flora are tropical and subtropical areas, in connection with which there is some probability that the moss mites inhabiting these territories derive from the Palaeogene. In particular, their disjunctive occurrence in the Oriental Province and Europe may indicate their Early-Tertiary age. The Oriental tropical vegetation had been separated from Europe by savanna-type vegetation in Central and Middle Asia since the upper Jurassic period (SINITSYN, 1962, Fig. 27). The migration of tropical elements was, however, possible in all probability through the uniform zone of subtropical vegetation in the belt of islands at the southern border of the then existing continent, from eastern Asia to England. Towards the end of the Palaeogene this zone underwent a division — as has already been mentioned — into the East-Asiatic part and the European part (SINITSYN, 1962). It was then that the ranges of moss mites living in a humid tropical climate and having a low ecological value in relation to humidity as well as representing the eury type in relation to temperature must have become disjoined.

(2) According to VUL'F (1944), nowadays the Early-Tertiary relicts may occur also on Madeira, in Colchis, and in the Lencoran Lowlands. However, as a number of later relicts are also found in these areas, only those may be regarded as the Palaeogene ones which, in addition, live in the subtropical

and tropical areas at the present time. Besides, the Early-Tertiary relicts should not occur in the Mediterranean today; otherwise they would be species with a high tolerance not only regarding temperature but also with respect to humidity and their localities in Colchis or in the Lenkoran Lowlands might be of quite recent date.

On the basis of the foregoing (1 and 2) I think that *N. anauniensis* CANESTRINI et FANZAGO (21) and *Q. quadricarinata* (MICHAEL) (102) existed perhaps as early as the Palaeogene. Now they both have Holarctic-subtropical ranges (Table XII).

(3) HAMMER (1965) was the first to give attention to the South-Pacific disjunction (South America — Australia and New Zealand) in moss mites and, basing herself on the WEGENER'S theory, referred its origin to the early Palaeogene. By this she established also the minimum age of *Mucronothrus nasalis* (WILLMANN). The later results of her researches (HAMMER, 1966) suggest that the South-Pacific disjunction in three other species, *E. minutissimus* (BERLESE) (2), *T. excavatus* (WILLMANN) (34), and *T. novus* (SELLNICK) (36), also originated in the early Palaeogene. The first of these species has a Holarctic-subtropical range now (Table XII) and is a forest mesopolyhygric form, whereas the other two have semicosmopolitan ranges and are stenotopes, associated with *Sphagnum* sp. (Table XIII). *T. excavatus* (WILLMANN) (34) occurs in Europe, South America, and New Zealand, but is absent from North America, which may indicate its Antarctic and therefore Palaeogene origin in South America.

On the whole, 20 species, i.e., 11·30% of the moss mite fauna of the Poznań region are, in all probability, of the Palaeogene age. In addition, several species (Tables XII and XIII), to be sure, do not show the typical South-Pacific disjunction, but occur also out of the Holarctic, in New Zealand. They may also be found in South America one day. For the present, the time of formation of their ranges has been determined on the basis of other characters, easier to establish in time, but it cannot be ruled out that in the future it will be necessary to acknowledge them as old Tertiary forms.

c. Range Characters Formed in the Neogene

By absolute standards the beginning of the Neogene took place about 25 million years ago and it ended about 600,000 years B. C. (SINITSYN, 1962). The second part of the Neogene is in particular characterized by strong tectonic activity and a cooling of climate and, consequently, the bioclimatic zonation became markedly complicated.

At the end of the Miocene and the beginning of the Pliocene coniferous forests with an admixture of deciduous trees dominated in western Siberia (west of the Yenisey) and in northern Europe (Baltic coast and Scandinavia). In eastern Siberia the spruce-fir taiga with a proportion of pine and hemlock-spruce, descending from the mountains, occupied more and more extensive areas and ousted the more thermophilous deciduous and coniferous species. In the Middle and Late Tertiary the Asiatic taiga had no constant connections

with the Canadian taiga (disappearance of the land bridge across Bering Strait), which extended in the west and in the east of North America, being united only in northern Canada. In the middle zone of the North-American mainland steppes penetrated deep into the taiga area. Since the Miocene the western portion of North-American coniferous forests had been developing to a great extent autonomically, owing to the intense action of mountain-building forces and sporadic occurrences of connections with Asia.

In Eurasia the deciduous-coniferous forest zone was bipartite, its range being more or less like that in the Late Oligocene. Its southern portion, however, did not contain tropical but only subtropical evergreen elements. In North America the deciduous forests of the temperate zone shifted as a rule to the south-west and only slightly to the south, along the Pacific coast and damp mountain valleys in the Miocene and Pliocene.

Steppes, deserts, and tropical forests of Eurasia had practically preserved their ranges since the Late Palaeogene. The process of continentalization continued in the area of dry climate (Kendeigh, 1961; Sinitsyn, 1962).

The following climatic-vegetative zones swept across Poland, from north to south, beginning at the early Miocene: the tropical-subtropical zone (Lower Miocene), the Mediterranean (subtropical and Mediterranean vegetation), the zone of warm-temperate deciduous and mixed forests, floristically classified as East Asiatic-North American (Upper Miocene and, partly, Pliocene), and the zone of deciduous forests of temperate climate (floristically Holarctic or Eurasian) in the Pliocene (Szafer, 1964).

The following facts are of basic significance in so far as the determination of the Neogene origin of the ranges of some moss mite species is concerned:

1. The existence and disappearance of land bridges between Asia and North America as well as between Europe and North America and the possibility of migration of the definite bioclimatic types by them.

2. The formation of the so-called European-Manchurian disjunction in the range of deciduous forests and animal species associated with them.

3. Relict localities of definite species in typical refuges of the Tertiary fauna: on Madeira, Sardinia and Corsica, in Colchis, Lenkoran Lowlands and some portions of deciduous forests in Asia, regarded as remnants of temperate Tertiary forests (Krivolutskiǐ, 1966b: Turgay forests).

The lasting land bridge between Asia and North America in the Bering region and as far to the south as the Aleutian Is. persisted throughout the Palaeogene. Arctic Tertiary coniferous-deciduous forests dominated then in this area (Kendeigh, 1961; Sinitsyn, 1962; Vul'f, 1944). During the whole Neogene and later, throughout the Pleistocene, the land bridge existed only periodically (Vul'f, l. c.). The spruce and fir became more and more distinctly dominant in the forests of the Bering region (Sinitsyn, 1962), but up to the end of the Miocene (Tolmachev, 1954) the forests composed of deciduous trees and members of the family Taxodiaceae had a continuous range in Siberia and in corresponding latitudes of North America. In the Pliocene the

climate of the remote northern areas became cooler and cooler and, consequently, this flora retreated more southwards to eastern Asia and the Atlantic portion of North America (SZAFER, 1964: 197—198).

In the case of the moss mites that did not spread northwards beyond the zone of temperate coniferous-deciduous forests and living now, among other places, in Japan and in the Atlantic part of North America, the East Asiatic-North American disjunction seems to have been developing also in the Pliocene, simultaneously with the formation of the Arctic Tertiary disjunction in the vegetation of the area under discussion. This refers to the following species: *N. coronata* BERLESE (41) — Table VIII, *G. bicostatus* (C. L. KOCH) (46) — T. VIII, *C. latus* C. L. KOCH (57) — T. VIII, *C. cepheiformis* (NICOLET) (58) — T. VIII, *F. quadripertitus* GRANDJEAN (67) — T. XIII, *O. subpectinata* (OUDEMANS) (99) — T. VIII, *C. gracilis* (MICHAEL) (132) — T. XII, *P. punctum* (C. L. KOCH) (141) — T. VIII, *S. latipes* (C. L. KOCH) (171) — T. VIII, *S. laevigatus* (C. L. KOCH) (172) — T. XIII.

The period when the land bridge between Europe and North America was broken may be an indication of the age of the North-Atlantic disjunction. It is known that the North-American shield had separated from the Baltic shield long before the period in question. However, since the species in which this disjunction occurs do not inhabit the subtropical and tropical zones at the present time, its formation can by no means be associated with the separation of the Baltic and North-American shields. Moreover, according to BUBNOFF (1956), the existence of the Atlantic between Canada, Greenland, and Scotland has not been proved for the Palaeogene, because the corresponding sea sediments are missing. Both the continents were probably linked by Greenland up to the beginning (VUL'F, 1944) or even the middle (A. S. KOSTROWICKI, oral information, 1967) or the Quaternary. The fossil flora which indicates a mean annual temperature of +8°C is known from the Eocene of northern Greenland and the first signs of frost in the present-day Arctic Province date back to the Upper Miocene (WALTER, 1954). As we are, above all, concerned here with the species reaching the boreal zone in the north (Table IX), the very beginning of the Miocene may roughly, be assumed as the time of the origin of their North-Atlantic disjunction, but it may be that it came to be as early as the end of the Palaeogene. Taking into consideration the floral material alone (Central-European and Scandinavian species in the North-American flora), VUL'F (1944) points out the necessity of admission of the occurrence of a direct junction between North America and Europe (out of the Arctic zone) as late as the beginning of the Quaternary. In SZAFER'S (1964) opinion, the northern transatlantic disjunction dates from the Pliocene. The formation of the North-Atlantic disjunction may be referred to the moment of interruption of the connection of the temperate and boreal zones between Europe and North America in the Neogene in the following species: *E. minutissimus* (BERLESE) (2) — Table XIII, *S. magnus* (NICOLET) (6) — T. IX, *P. globosus* (C. L. KOCH) (9) — T. IX, *P. italicus* (OUDEMANS) (10) — T. VIII,

P. piger (SCOPOLI) (13) — T. VIII, *E. cribrarius* (BERLESE) (15) — T. VIII, *C. segnis* (HERMANN) (24) — T. XIII, *M. gracilis* VAN der HAMMEN (35) — T. IX, *T. glaber* (MICHAEL) (37) — T. IX, *N. nanus* (NICOLET) (39) — T. IX, *N. elegantula* BERLESE (42) — T. IX, *M. papillipes* (NICOLET) (54) — T. IX, *A. ovatus* (C. L. KOCH) (70) — T. IX, *C. coriaceus* (C. L. KOCH) (76) — T. IX, *C. areolatus* BERLESE (77) — T. IX, *C. minusculus* BERLESE (82) — T. IX, *P. bella* (SELLNICK) (125) — T. IX, *O. calcarata* (C. L. KOCH) (127) — T. IX, *C. gracilis* (MICHAEL) (132) — T. XII, *C. mediocris* BERLESE (133) — T. XII, *F. fuscipes* (C. L. KOCH) (136) — T. VIII, *F. setosus* (C. L. KOCH) (137) — T. VIII, *T. novus* (SELLNICK) (140) — T. IX, *G. elimata* (C. L. KOCH) (156) — T. XII, *P. nervosa* (BERLESE) (158) — T. XII, *A. longipluma* (BERLESE) (160) — T. IX, *L. humerata* SELLNICK (170) — T. IX, *X. capucinus* (BERLESE) (176) — T. XIII.

In addition to the species that in the north reach the boreal bioclimatic zone, the fauna under study contains a number of species which occur also in the Arctic. The arctic flora began to develop from the arctic Tertiary elements as early as the Miocene (KENDEIGH, 1961; VUL'F, 1944). Though the species of moss mites with which we are concerned here extend to the Arctic, their basic ranges stretch in the temperate, boreal, and even submeridional zones. They are therefore species which probably existed before the formation of the arctic zone. When the temperate and boreal zones had retreated southwards, they may have remained in the place owing to their great tolerance of low temperatures and, thus, went to the making of the arctic fauna (KENDEIGH, 1961). Exchange between North America and Europe was possible for them far longer than for more thermophilous species; it proceeded along two ways (VUL'F, 1944): for more arctic elements through northern Greenland and Spitsbergen and for moderately arctic specimens via Greenland and Iceland. The ranges of the species that reach the Arctic and now live in Europe and northern part of North America but are absent in Asia and Alaska seem to have been developing up to the very end of the Neogene. An additional criterion of this hypothesis may be the occurrence in Greenland and Iceland. The following species can be mentioned in this group: *N. silvestris* NICOLET (23) — Table XII, *H. thori* (BERLESE) (29) — T. XI, *P. peltifer* (C. L. KOCH) (31) — T. XIII, *T. velatus* (MICHAEL) (86) — T. XI, *O. nova* (OUDEMANS) (95) — T. XIII, *O. ornata* (OUDEMANS) (96) — T. X, *O. unicarinata* (PAOLI) (101) — T. X, *A. coleoptrata* (L.) (122) — T. X, *P. willmanni* VAN der HAMMEN (124) — T. XI, *P. pilosus* HAMMER (174) — T. XI.

In all probability, the North-Atlantic disjunction (Table XI) in *T. foveolatus* WILLMANN (38) and *A. latitecta* (BERLESE) (126), also got into shape towards the end of the Neogene, but their distribution does not reflect this fact to the full. Surely, they are both northern elements in the fauna under study, but the first of them occurs only in Greenland (though in both its eastern and the western part) and the other only in North America exclusive of Greenland. It is hardly probable that they have been brought along by man, because

T. foveolatus WILLMANN (38) is a typical dweller of moist and wet mosses and *A. latitecta* (BERLESE) (126) lives in both south-eastern and northern parts of North America.

The origin of species showing the European-Manchurian disjunction should be associated with the history of the development of the Turgay flora. This flora had differentiated from the mesophilous vegetation in the north of Asia as a result of the progressive cooling of climate and consisted of deciduous trees and thermophilous conifers *(Taxodiaceae)*. In the opinion of most of the authors (VUL'F, 1944; TOLMACHEV, 1954; KRYZHANOVSKIĬ, 1965; MARKOV et al., 1965), the Turgay forests reached the peak of development in the Miocene and then had a continuous range north of the line running across northern Kazakhstan, northern Mongolia, and the Amur region. As has already been mentioned, these forests swept over Central Europe in the Upper Miocene and Pliocene (SZAFER, 1964). According to the above-mentioned authors, the disjunction between the European and East-Asiatic portions of the Turgay flora began to develop as late as the Pliocene. Only SINITSYN (1962) refers the maximum development of the Turgay forests to the Oligocene and the formation of the disjunction in question in the territory of southern Siberia and in Mongolia to the Miocene. The deciduous forests re-developed in Eurasia during the Eemian interglacial. However, there was most probably a gap in Transbaykalia, occupied by steppes and the so-called open taiga, between the Siberian and Far-East areas of deciduous forests or those with a great admixture of deciduous trees (BOYARSKAYA, 1965, p. 427). Thus, the disjunction in the species inhabiting the deciduous (mesophilous) forests of the temperate zone between Europe and eastern Asia should be considered to be Neogene age. In the material under study this disjunction has been found in the following species: *H. targionii* (BERLESE) (28) — Table VII, *N. coronata* BERLESE (41) — T. VII, *C. latus* C. L. KOCH (57) — T. VIII, *C. cepheiformis* (NICOLET) (58) — T. VIII, *G. fusifer* (C. L. KOCH) (60) — T. VII, *F. quadripertitus* GRANDJEAN (67) — T. XIII, *X. clypeator* ROBINEAU-DESVOIDY (71) — T. VII, *C. falcata* EVANS (74) — T. VII, *C. pusillus* (BERLESE) (148) — T. VII, *H. initialis* (BERLESE) (168) — T. XIII. Numerous European-Manchurian species of pre-Quaternary age are also mentioned by HORMUZAKI (1930).

A disjunction analogous to the European-Manchurian one seems to exist in the species inhabiting the temperate and boreal bioclimatic zones and reaching the Arctic but absent from the region of continental climate today. I mean the species which in the Arctic occur, above all, in the coastal tract of Greenland, in the climate influenced by the Atlantic, or in a similar situation in Canada or Alaska. Since throughout the Tertiary the climate of Asia underwent a more and more intense continentalization and in the Quaternary resembled the recent climate in this respect, these species cannot have lived in Siberia during the glaciations. Hence also in their ranges the above-mentioned disjunction originated in the Neogene, perhaps in the late Pliocene. It presumably arose then in the following species: *H. rufulus* C. L. KOCH (1) —

Table X, *E. minutissimus* (BERLESE) (2) — T. XIII, *R. ardua* (C. L. KOCH) (16) — T. XIII, *N. anauniensis* CANESTRINI et FANZEGO (21) — T. XIII, *N. pratensis* SELLNICK (22) — T. X, *C. biurus* (C. L. KOCH) (25) — T. X, *C. spinifer* (C. L. KOCH) (27) — T. X, *H. paolianus longisetosus* WILLMANN (30) — T. X, *T. tectorum* (BERLESE) (32) — T. X, *Q. quadricarinata* (MICHAEL) (102) — T. XIII.

Detached localities of several species in the pistachio and nut forests of the Tashkent region are related to the European-Manchurian disjunction (KRIVOLUTSKIĬ, 1966b). They are regarded as remains of the Turgay forests, subsisting on the slopes of mountains owing to a more favourable local total of rainfall. Their isolation goes back to the period of formation of the European-Manchurian disjunction. A number of insect species (KRYZHANOVSKIĬ, 1965) whose ranges were originally continuous throughout Asia and are amphipalaearctic nowadays (with a disjunction in Middle and Central Asia) have subsisted in these forests since the Neogene. The there encountered moss mites, which occur nowhere else in the region of continental climate at the present time, have probably also been isolated in the forests in question since the Lower or Upper Neogene, according to their tolerance of temperatures. The following species are included in this group: *R. ardua* (C. L. KOCH) (16) — Table XIII, *T. tectorum* (BERLESE) (32) — T. X, *F. quadripertitus* GRANDJEAN (67) — T. XIII, *X. clypeator* ROBINEAU-DESVOIDY (71) — T. VII, *X. permixtus* (ANDRÉ) (72) — T. II, *C. femoralis rugosior* BERLESE (79) — T. VI, *C. sellnicki* RAJSKI (135) — T. VI, *L. similis* (MICHAEL) (169) — T. X, *X. capucinus* (BERLESE) (176) — T. XIII.

Owing to the lack of fossil material the characteristics of the range or, to be more exact, the latest probable time of their formation can be the only reliable indication of age, but it is obvious that the species whose range underwent a disjunction at a definite time must have existed before. TOLMACHEV (1954), for instance, determined the maximum age of the species with the European-Manchurian disjunction at the beginning of the Palaeogene and their minimum age at the end of the Miocene.

The age of species can also be indicated, in addition to disjunctions, by their relict localities. In our case, they are areas which owing to the topical circumstances have preserved their climate and vegetation hardly changed since the Neogene, while in the adjacent territories both the climatic conditions and the plant cover went many a time through a complex evolution. The members of the fauna under study have such relict localities on Madeira, Sardinia and Corsica, in Colchis and in the Lenkoran Lowlands. Naturally, in these regions only the localities of the species that in the surrounding areas have died out in consequence of the changes of climate and, what follows, those of the flora, may be regarded as the relict ones.

In WALTER'S (1954) opinion, the vegetation on Madeira is similar to that in the warm and humid climate of Central Europe in the Miocene. A number of evidences for the Tertiary age of the Madeiran flora are given by VUL'F

(1944). According to this author, the Canary Is. are the extension of the Atlas Mts. and were directly connected with Morocco. Their flora and, consequently, probably also the moss mite fauna, are, to a great extent, of Tertiary European-North African origin. Later, when the land connection of the Canary Is. with Africa had been broken and the climatic conditions in the Mediterranean favoured the development of xerophytes, the mesophilous flora and fauna perished in the nearly whole Mediterranean, being preserved only in a few places, among them also on Madeira. Thus, the moss mite species which occur in the temperate zone of Europe and, being absent in the Mediterranean, have their localities on Madeira, probably had a continuous range in North Africa and Europe in the Upper Miocene.

It may also well be that the relictual species on Madeira are of Pliocene or even Quaternary age, in which periods they lived in Europe in a climate resembling the recent one. During the glaciations they migrated southwards and occupied the Mediterranean area in the phases of pluvial climate. In the interglacials they returned to the north, in the Mediterranean remaining only in places where the humid climate had subsisted (Madeira). This hypothesis is, however, less probable, since it implies the necessity of long migrations, rather impossible as regards Madeira and the Azores in the Quaternary, as there was no land connection between them and the mainland. Moreover, some other characteristics of the ranges of the species in question also took origin in the Neogene.

In the light of the available data the following species of the fauna examined have their relict Upper-Miocene localities on Madeira: *S. applicatus* (Sellnick) (4) — Table I, *P. lentulus* (C. L. Koch) (11) — T. IV, *O. subpectinata* (Oudemans) (99) — T. VIII, *P. punctata* (Nicolet) (123) — T. XI, *C. mediocris* Berlese (133) — T. IX, *C. borealis* (Trägårdh) (147) — T. IX.

Another region of the Mediterranean in the wide sense (or the so-called Old Mediterranean) with which we are concerned here and in which the Neogene elements of climate, flora and fauna have been preserved to a great extent is Transcaucasia (Szafer, 1964): Colchis, Talish, and the Lenkoran Lowlands. Since the paper in which the moss mites of the Talish Mts. are described (Kuliyev) is not available for me, I shall confine my considerations to Colchis and the Lankoran Lowlands. Krivolutskiĭ (1966a) has recently published a list of moss mites of these regions. They have not been included in the faunistic survey (Rajski, 1967, 1968).

To the middle of the Pliocene the flora of Colchis and the Lenkoran Lowlands developed quite independently of the vegetation of the Russian Lowlands, from which it was separated not only by the Caucasus but also by the sea. Earlier than with Europe, the Caucasus had a land connection with western Asia (towards the end of the Miocene) and so was joined with the remaining part of the Old Mediterranean. Besides many other relicts, the Transcaucasian localities (Vul'f, 1944) have also those of the Turgay (Neogene) flora. These are mesophilous forest species that may occur also in other typical refuges

of the Neogene flora and fauna in south-eastern Asia and in the east of North America. However, they do not live in the areas of the typical Mediterranean climate now. In the Quaternary the boreal elements did not reach the Lenkoran Lowlands and only to a low degree Colchis (Vul'f, 1944). Therefore, the mesophilous forest species of the fauna under study, whose origin should be referred to the development of the Turgay forests (Kryzhanovskiĭ, 1965) have very likely their relict sites in this region and these sites date back, in all probability, to the end of the Miocene and the beginning of the Pliocene. Naturally, only the localities of the species that owing to their ecological characters could not reach this region under modern climatic conditions may be regarded as relicts. The following species seem to satisfy this condition: *S. magnus* (Nicolet) (6) — Table IX, *S. striculus* (C. L. Koch) (8) — T. X, *P. italicus* (Oudemans) (10) — T. VIII, *P. ligneus* Willmann (12) — T. IX, *N. nanus* (Nicolet) (39) — T. IX, *H. punctulata* Berlese (44) — T. IV, *Z. micronychus* (Berlese) (61) — T. IV, *A. polonicus* Kulczyński (66) — T. V, *A. ovatus* (C. L. Koch) (70) — T. IX, *C. femoralis* (Nicolet) (78) — T. I, *C. femoralis rugosior* Berlese (79) — T. VI, *O. bicarinata* (Paoli) (89) — T. VI, *Q. quadricarinata* (Michael) (102) — T. XIII, *E. occultus* (C. L. Koch) (119) — T. VI, *P. punctata* (Nicolet) (123) — T. XI, *M. pseudofusiger* (Schweizer) (145) — T. I, *C. voigtsi* (Oudemans) (151) — T. V, *P. tenuiclava* (Berlese) (159) — T. VIII, *X. variabilis* (Rajski) (177) — T. V.

The occurrence of any species on Corsica and Sardinia as well as in Europe, out of the Mediterranean, may indicate the relictual character of the localities on these islands. Their flora is composed mainly of Miocene elements (Vul'f, 1944). Sardinia and Corsica most likely maintained a direct land connection with each other and with the Iberian and Italian Peninsulas as late as the end of the Miocene and the beginning of the Pliocene.

Probably only *R. duplicata* (Grandjean) (17) — Table II — has subsisted on Corsica since the time of its being directly connected with the Iberian and Italian Peninsulas. The other two species of the moss mite fauna of the Poznań region occurring on Corsica, *E. silvestris* (Forsslund) (65) and *S. laevigatus* (C. L. Koch) (172), are also well represented in the Mediterranean. As a result, it cannot be established for how long they have been going into the making of the fauna of this island.

An analysis of the ranges shows that in 77 species, i.e., 43·50% of the fauna under study (Table XIX), they have characters which may have developed in different periods of the Neogene, from the early Miocene (North-Atlantic disjunction in the species of the temperate and boreal zones) to the late Pliocene (the same disjunction in the species reaching the Arctic zone). As it has appeared, the ranges of some species were formed both in the Palaeogene and in the Neogene. In a number of species not one but several characteristics indicate the formation of their ranges in the Neogene (Table XIX).

d. Range Characters Formed in the Quaternary

The Quaternary covers the last 600,000 years of geological history. From

the viewpoint of formation of the ranges of moss mites the most important events of the Quaternary were strong climatic oscillations, which most likely caused the fourfold glaciation in the Northern Hemisphere. Uniform icecaps covered North America and Europe, probably including western Siberia, whereas the eastern part of Siberia had only local mountain and valley glaciers owing to the advanced continentalization of its climate (Markov et al., 1965).

Towards the end of the Neogene and at the beginning of the Quaternary tundra appears for the first time in the history of the Earth. It originated in north-eastern Asia and in the northern part of North America. Before the first glaciation Siberia was still covered by taiga, spruce-fir taiga in the west and north-west and larch taiga on the Central Siberian Plateau. Deciduous forests had persisted till the glaciations only in some regions of the Altai, Kuznetsk Ala-Tau and Transbaykalia. On the other hand, in the region of the middle course of the Amur, in northern and north-eastern China, Korea and Middle Japan they existed throughout the Quaternary (Sinitsyn, 1962).

Tundra and taiga occupied the whole northern part of North America at the beginning of the Pleistocene and next, as the icesheet expanded, they underwent destruction. Both these formations were preserved in Alaska throughout the glaciations and, in addition, in the Quaternary this refuge had a periodical connection with north-eastern Asia and was isolated by the icesheet from the other North-American refuges. There was a possibility of exchange of species fit for life in the Arctic tundra and, perhaps, in the taiga, owing to this periodical connection between Asia and North America in the Quaternary. Tundra may have subsisted on the Arctic Archipelago during the glaciations, whereas the coniferous forests were also preserved in the northern portion of the Rocky Mts. and on the Pacific coast of North America, as well as farther to the south, in the mountains but at lower altitudes.

In the eastern part of North America coniferous forests encroached upon the region of the northern Appalachian Mts. and there they mingled with deciduous forests. Tundra covered also a narrow tract in the foreland of the icesheet, where it had an admixture of steppe, mountain and even forest elements.

Deciduous forests persisted in the eastern part of North America in the territories which they had occupied as early as the Neogene. Their structure also remained unchanged. Only in the northern regions they had been enriched in taiga elements (Kendeigh, 1961).

The ice-cap attained the relatively greatest extent in Europe and, since it leaned more or less against the mountains which have a parallel course, the flora and fauna, resembling those of eastern Asia and North America at the beginning of the Pleistocene, became more and more impoverished during the consecutive glaciations. In the Mediterranean, where the thermal conditions did not change essentially, the successive glaciations were marked by periods of pluvial climate and the interglacials by a climate favouring the development of xerophytes.

As will be seen from the previous considerations on the formation of ranges of the moss mites, a large number of species that occur in the Poznań region today originated in the pre-Quaternary periods. As the Wielkopolsko-Kujawska Lowlands were overcome by all the four glaciations, these species must have lasted out the unfavourable climatic periods somewhere in the European territory, because their European populations had already no connections with the East-Asiatic or North-American populations. Although it is impossible to point to the refuge from which these species came back to Central and North Europe in the interglacials and Holocene, the existence of such refugial areas must be assumed to obtain a full picture of bioclimatic conditions of the Quaternary in Europe.

A map showing the boundaries of the maximum ranges of the icesheet and vegetation zones in Europe is given, among other workers, by Flint (1957) and Walter (1954), and I shall not discuss it here in detail. However, it must be kept in mind that some species, which now reach the boreal and Arctic bioclimatic zones, were able to survive both in small refuges with relatively mild local climatic conditions within the area of glaciation and at a short distance from the glacier margin, as well as in areas covered with forests at the time of the glaciations.

The present conditions in Greenland and, partly, in Alaska are an indirect evidence of the possibility of survival of species not only from the Arctic zone but also those from the temperate zone in the region of glaciation. Greenland is at a glacial stage now, and only its narrow coastal tract is free of ice. Its flora consists of about 416 species of higher plants (Vul'f, 1944), out of which 67% constitute a temperate element, 24% form the flora of deciduous forests, and 18% reach southwards to Labrador. Birches and alders form exuberant shrub thickets here. At places, the Malaspina Glacier in Alaska covers quite a vigorous spruce forest and that of *Alnus viridis* (Chaix) Lam. et D. C. In the European parts of the U.S.S.R. the taiga neighboured almost directly on the glacier margin (Minyaev, 1965) and, according to some authors (Markov et al., 1965), the elements of deciduous and spruce forests could survive not far from it. These facts suggest that in the European territory there may have existed detached places in which the influence of the icecap was very small during the glacial periods. An analysis of the contemporary flora (Vul'f, 1944) allows the supposition that there were local refuges in northern Iceland and in north-eastern Europe (Minyaev, 1965). Moreover, there are data which indicate the local survival of the late Tertiary flora, among other places, in the Carpathians. More extensive refuges are situated in southern France, in the Balkans (locally even in Croatia and Slovenia), as well as in the area which stretches from the Podolian Plateau up to the southern ridges of the Ural Mts. There are also many refuges which had preserved the Tertiary flora but did not constitute centres of expansion for all the extant species in the Holocene (e.g., Strandzha Mts. in the Balkans).

Contrary to the earlier opinions (Hormuzaki, 1930), the latest studies

carried out in Romania have shown that in the glacial periods the climate was subarctic there and for this reason only some species of the genus *Pinus* L. had a good chance to last out the glaciation, the same being true of *Larix* Mill. and *Juniperus communis* L. in the Pannonian Lowlands. Different species of *Salix* L. and *Betula* L. and, perhaps, *Populus tremula* L. and *Alnus incana* (L.) Mnch. subsisted on the inner slopes of the Carpathian range, whereas the possibility of existence of local refuges containing elements of mixed oak forest (*Quercus* L. and *Corylus* L.) in Romania lies in the sphere of conjecture only (Pop, 1964).

A typical Holocene cycle of forest development has also been found in France, Austria and Hungary, Bohemia and Moravia, as well as at the foot of the southern slopes of the Alps. The forest-building species of broad-leaved trees were preserved only in southern Europe. The modern discontinuous mountainous ranges of the beech in Spain provide evidence of its continuous range in this region in the glacial periods, and the only place in Europe where the oak dominated as early as the turn of the Preboreal was Mljet Island in southern Dalmatia (Firbas, 1964).

Thus, in spite of the obvious impoverishment of the European flora and fauna, some of the species managed to survive this indubitable disaster at a fairly short distance from Poland or, perhaps, even within the area of this country. In the territories affected by glaciation their ranges, though showing some Tertiary characters, were certainly being formed up to the recent epoch. There is also a group of species whose ranges can be explained exclusively in connection with the Quaternary.

As has already been mentioned above, the land connection of North America with Asia in the Bering region existed periodically during the glaciation and, consequently, the species that tolerate climatic conditions of the Arctic and, perhaps, the boreal zone could at that time at latest move in the east-west direction (Kendeigh, 1961). A trace of the migrations may be the present-day occurrence of these species in Alaska and north-eastern Asia and in many cases only in Alaska or northern Canada because of our better knowledge of these areas. The following species may be mentioned here: *H. rufulus* C. L. Koch (1) — Table X, *P. ligneus* Willmann (12) — T. IX, *R. ardua* (C. L. Koch) (16) — T. XII, *E. ribagai* Berlese (19) — T. X, *N. anauniensis* Canestrini et Fanzago (21) — T. XII, *N. pratensis* Sellnick (22) — T. XII, *C. segnis* (Hermann) (24) — T. XIII, *C. biurus* (C. L. Koch) (25) — T. X, *C. horrida* (Hermann) (26) — T. XI, *C. spinifer* (C. L. Koch) (27) — T. X, *H. paolianus longisetosus* Willmann (30) — T. X, *P. peltifer* (C. L. Koch) (31) — T. XIII, *T. novus* (Sellnick) (36) — T. XIII, *C. bipilis* (Hermann) (68) — T. XII, *C. labyrinthicus* (Michael) (80) — T. XI, *O. translamellata* (Willmann) (100) — T. X, *Q. quadricarinata* (Michael) (102) — T. XII, *A. longilamellata* (Michael) (108) — T. VIII, *B. lanceolata* (Michael) (106) — T. X, *T. latirostris* (C. L. Koch) (131) — T. X, *C. gracilis* (Michael) (132) — T. XII, *C. borealis* (Trägårdh) (147) — T. IX, *N. aurantiacus* (Oudemans)

(154) — T. X, *O. tibialis* (Nicolet) (161) — T. X, *Z. exilis* (Nicolet) (162) — T. X, *L. similis* (Michael) (169) — T. X, *S. pallidulus* (C. L. Koch) (173) — T. XII.

Until quite lately the age of the European-Manchurian disjunction was referred exclusively to the Neogen. Since the map of the vegetation of Asia in the Eemian interglacial was published (Boyarskaya, 1965), it has been known that at any rate the forest species that can occur also in steppes or at least in coniferous forests could have a continuous range from Europe up to eastern Asia for the last time in the Eemian interglacial. In these species the European-Manchurian disjunction must be considered to be Quaternary in age. I found five such species in the material under study: *D. (P.) clavipes* (Hermann) (48) — T. VII, *X. badensis* (Sellnick) (175) — T. VII, *G. bicostatus* (C. L. Koch) (46) — T. VIII, *S. latipes* (C. L. Koch) (171) — T. VIII, and *C. gracilis* (Michael) (132) — T. XII. Since the other characters of the ranges of the last three species were formed in the Neogene, only the minimum age of the first two species may be estimated as Quaternary.

The so-called interpolar Holarctic-Andine disjunction was also finally formed in the Quaternary. Elements of the temperate zone penetrated into South America in the Eocene and later, at more or less marked intervals, up to the end of the Pleistocene. They migrated, above all, from north to south along the ranges of mountains, in the west of North and South America. So far, it is impossible to conceive of how they covered the 600-kilometre distance in the Panama Isthmus, where there are no elevations even approaching to 1000 m. in altitude, though this part of the route may well have been higher once. Absolute evidences for the migration from the north are the intermediate localities of higher plants and lack of some species in Patagonia and Terra del Fuego, where they would have to be present if they were derived from the south. Such migrations were possible owing to the oscillations of the equator by about 50° on the axis of both American continents. Now the timberline in the Andes runs at an altitude ranging from 3000 to 3800 m. (Szafer, 1964; Vul'f, 1944) and at places even at 4500 m. (A. S. Kostrowicki, 1967, oral information). The Holarctic-Andine disjunction may have been formed in moss mites at the same time as in higher plants. Until recently it could indicate only a Quaternary age of the moss mites. It is however known at present that part of the species which have this disjunction show also the South-Pacific disjunction and, consequently, they lived in South America as early as the Palaeogene. Thus, the number of the species whose origin in the Quaternary is evidenced by their Holarctic-Andine disjunction may decrease with the progress of investigations of the moss mite fauna in Australia and, especially, in New Zealand.

In the meantime the Quaternary age of the Holarctic-Andine disjunction can be established in the following species: *C. segnis* (Hermann) (24) — Table XIII, *O. nova* (Oudemans) (95) — T. XIII, *C. gracilis* (Michael) (132) —

T. XII, *S. pallidulus* (C. L. Koch) (173) — T. XII, *X. capucinus* (Berlese) (176) — T. XIII.

Some species of the fauna under study have their ranges confined exclusively to the areas covered by the ice during the glacial epoch or affected directly by the Arctic climate. These ranges must have developed thoroughly in the Quaternary times and, in the case of some of them, even in the Holocene. According to the present state of our knowledge of the distribution of moss mites, these species are as follows: *P. tardus* Forsslund (14) — Table V, *T. nigricans* Willmann (33) — T. III, *D. (S.) boreus* Bulanova-Zakhvatkina (50) — T. III, *O. falcata marginedentata* Strentzke (91) — T. III, *O. sigma conjuncta* Strentzke (98) — T. III, *L. ciliatus foveolatus* Willmann (110) — T. III, *L. rugosus* (Sellnick) (111) — T. II, *E. hygrophilus* (Knülle) (118) — T. III, *E. gessneri* Willmann (165) — T. III. Some of them belong to abundant genera whose species not only stand close to each other morphologically but, in addition, are differentiated into subspecies and show great variation, which may be regarded as characters pointing to their young phylogenetic age (Holmuzaki, 1930, and others).

It is worth while to emphasize that three of these forms occur in bog mosses only, and therefore in cold environments, two are evidently associated with deciduous forests, and one with coniferous forests.

To sum up, in 47 cases the ranges examined were partly formed in the Quaternary. However, the ranges of most of the species in question originated in earlier periods, above all, in the Neogene. Only 20 species, or 11·30% of the fauna examined have such ranges that their whole development may, according to our present knowledge, be referred with a great probability to the Quaternary (Tables II, III, V, VII, X, XII, XIII, and XX).

e. General remarks

The historical-geographical analysis of the ranges of species belonging to the moss mite fauna of the Poznań region failed to demonstrate any distinctive range characters that could be referred to a definite historical moment, in about 60 species, which form 33·90% of the fauna examined. As can be seen from Table XXI, they are for the most part European and Palaearctic species. Nowadays they inhabit both the territories that were affected by the Quaternary glaciation or the influence of the arctic climate and the areas in which they were possibly able to survive one or more glacial periods. They may be both pre-Quaternary and Quaternary species. It may well be that further faunistic studies will allow the discovery of unknown localities of these species, having a decisive effect on the determination of their age.

Although in some cases certain fragments of ranges have been assigned successfully to definite historical moments, other portions of these ranges indicate that, in all likelihood, on the one hand, our present knowledge of the range is incomplete and, on the other hand, a better knowledge in this respect may cancel the present estimate of the age of the given species. There are at least over a dozen such species. Here I shall mention only the most typical

ones. Two species, *P. ligneus* WILLMANN (12) and *C. borealis* (TRÄGÅRDH) (147), occur in Europe and Alaska (Table IX) furthest to the north in the boreal zone. These species have probably a North-Pacific disjunction, i.e., they ought to be found also in Asia. It will not be possible to determine the age of this disjunction exactly till they have been found there. However, it is most likely of pre-Quaternary origin. Four species, *N. anauniensis* CANESTRINI et FANZAGO (21), *N. silvestris* NICOLET (23), *P. peltifer* (C. L. KOCH) (31), and *F. quadripertitus* GRANDJEAN (67) (Tables XII and XIII), live in the Holarctic and New Zealand. Presumably, they will also be found in South America, and then we shall be in a position to determine their age on the basis of the South-Pacific disjunction, namely, as Palaeogene. So far, the age of one of them has been established in this way on the basis of its occurrence in Baltic amber. It is a noteworthy fact that 3 of these species have a relatively low position in the phylogenetic system. Two species, *T. excavatus* (WILLMANN) (34) and *H. initialis* (BERLESE) (168), have not been found in North America hitherto, though, besides Europe, they occur in South America (Table XIII). Finally, two species have scattered ranges, which probably cannot be explained by a historical-geographical analysis. These are *R. ardua* (C. L. KOCH) (16), which occurs in the Holarctic and Polynesia (Table XII), and *T. sarekensis* TRÄGÅRDH (87), known from Europe, Greenland and the Hawaiian Islands (Table XIII). The first of them also occupies a distinctly low position in the phylogenetic system.

In general, one should expect that with the progress of study particular species will pass from one age group to another, but I hope that the general proportions of particular age groups (Table XXI) have been determined correctly.

The generalized results from the analysis carried out are given in Table XXI. According to them, the bulk of the moss mite fauna of the Poznań region (43·50 %) consists of the species whose ranges were formed in the Neogene and thus before the Ice Ages. It is interesting, because the Poznań region went through all the glacial periods and its fauna was destroyed at least three times. At the same time, the authors of most biogeographical-historical publications lay stress on the young age not only of the flora and fauna but also of the greater part of their components in areas once covered by the icesheet. The Palaeogene and Quaternary species occur in equal proportions in the fauna under study (11·30 % either group). Thus, the total of species of supposedly Tertiary age forms nearly 55 %.

The explanation of this situation should be sought for in the ecology of the species examined. Tables I—XIII show that most of the moss mites living in the Poznań region occur in several bioclimatic zones. Another remarkable detail are the wide ranges of moss mites, in most of the cases examined extending beyond the area covered by ice during the heaviest glacial period. The occurrence in different bioclimatic zones and the extensive ranges in a very large number of moss mite species result probably, among other things, from

the fact that soil temperature is liable to far smaller zonal fluctuations than air temperature (NAUMOV, 1961). Hence, soil-inhabiting animals find more homogeneous ecological conditions over far larger areas than the atmobios, and the same is true for humidity. Attention should also be given to the fact that moss mites are small animals and their habitat may be any, in the full sense of the word, microbiotope, provided it has a sufficiently high temperature and humidity and can supply them with food in the form of organic remnants. The above-mentioned local refuges within the region of glaciation presented a great many such microbiotopes.

The remarkable predominance of the western and southern elements over the eastern element among the European species and that of the European-West Siberian element over the remaining ones among the Palaearctic species (Table XIV) support the view that it was possible for a large number of moss mite species to survive the Ice Age in Europe.

In the light of the foregoing remarks it seems probable that the moss mite fauna of the Poznań region is composed chiefly of the species that survived the glacial epoch in Europe and in the Holocene recolonized the areas from which they had been ousted several times in the Quaternary. HORMUZAKI (1930) expresses an analogous opinion in his publication on the historical development of the butterfly fauna of Europe. According to him, the modern European fauna of butterflies consists of elements that lived out the Quaternary without moving away and, only to a very small extent, of immigrants from Asia. It is the more striking, because butterflies, being more directly associated with higher plants, were in a much worse situation in the Quaternary than moss mites. KÜHNELT (1961) emphasizes that the whole soil fauna is marked by its very high phylogenetic age, reflected, among other things, by the relatively wide ranges of its species. WARNECKE (1958) claims that in Europe only the species which now occur nowhere but within the area that was glaciated in the past may be of Asiatic origin. The rest of the European fauna, impoverished in the Pleistocene, redeveloped autonomously in the Holocene. As we already know that moss mites with ranges confined merely to the area affected by glaciation are very few in the fauna under study (Table XX), the views of WARNECKE (1958) must also be regarded as supporting the results obtained from the present work.

However, a number of authors hold the opinion that the fauna of the region in question is of relatively young age. Among other workers, BARTENEF (1934), whose so-called „northern part of the Palaearctic" includes also the Poznań region, thinks that the fauna of this region consists chiefly of species of glacial and interglacial origin. These species are said to have isolated systematic positions, because either they evolved rapidly or the forms most closely related to them became extinct. At any rate, such species are very few in the moss mite fauna of the Poznań region. In his paper on the origin and composition of the Middle Asiatic fauna KRYZHANOVSKIĬ (1965) emphasizes that the discontinuity of ranges in the Neogene (he means the European-Manchurian

disjunction) induced speciation in most of the cases and that now we mainly meet with genera having discontinuous ranges, whereas species of this type are very rare. Botanists, too, assert in general that a disjunction developed in the Neogene usually adds to the formation of vicarious species (TOLMACHEV, 1962, and others). KRYZHANOVSKIĬ (1965) however based himself, above all, on insects, especially, on those not belonging to the soil fauna, which is, in his opinion, poorly known in Middle Asia. On the other hand, as I have emphasized above, the soil fauna and, consequently, moss mites are a conservative group, and in the light of the present state of knowledge of their ecology they live in a more stable biotope than the epigeic insects.

In connection with the foregoing it seems that the results obtained from the historical-geographical analysis of moss mite ranges in this work may be acknowledged to be no less probable than the results of considerations of this kind in general, provided the specificity of this group has been allowed for.

6. The Postglacial History of the Moss Mite Fauna of the Poznań Region

On account of the poverty of fossil material (SØGAARD, 1938) an attempt to reconstruct the postglacial history of the moss mite fauna can be based only on the knowledge of the development of the given habitat, on the one hand, and the ecological requirements of particular species, on the other hand. The development of the geographical environment of the Poznań region, especially during the Holocene, is fairly well known. The ecological requirements of individual species, at any rate those forming the bulk of the fauna examined, have also been studied in outline. It would thus seem that the harmonious juxtaposition of these two known elements, and this is the main purpose of this section, will solve the problem. Unluckily, in this manner we merely approximate somewhat to the solution, because it is only to some extent probable that the species appeared in the study area in accordance with their ecological requirements as well as with the development of the environment, for it is well-known that particular tree species were usually locally present in an area long before they had attained their dominant position in it (WALTER, 1954). Besides, the typical Holocene succession of forest vegetation differs from both the vertical and the horizontal zonation of the modern flora (FIRBAS, 1964). Therefore one must make allowance for some deviations in the appearance of particular species in the region examined in both directions on the time scale. None the less, I hope that the essential moments in the development of the moss mite fauna of the Poznań region may be brought out appropriately by the use of the method which has been described above and is the only available one under present conditions.

The environs of Poznań were covered by ice for the last time during the second (i.e., Poznań-Dobrzyń or Frankfuhrt) phase of the main stadial of the Baltic Glaciation (Würm = Waldei = Wisconsin). The edge of the ice-sheet ran at a distance of several to some dozen kilometres north of Poznań. This

therefore seems to be the right moment to begin the history of the development of the fauna in the Poznań region. According to Książkiewicz and his collaborators (1965) all the three phases of the main stadial of the Baltic Glaciation, including the Oldest Dryas, covered a period from 29,000 to 12,500 years ago by the absolute time scale. (I give all dates according to the absolute time scale, counting backwards from the year 1965).

The whole postglacial history of the Poznań region is divided into the Late Glacial and the Holocene. The following periods can be distinguished in the Late Glacial epoch: Oldest Dryas, Bölling interstadial, Older Dryas, Alleröd interstadial, and Younger Dryas.

The Oldest Dryas lasted from the withdrawal of the ice-sheet to the appearance of the first birch trees. During this period the climate developed from arctic to subarctic; it was cold and continental, and the highest July mean temperatures fluctuated about +10°C. Up to 16000 years ago the area under study was covered by tundra, in which frozen glacial debris dominated over vegetation. Tundra with continuous coverage of mosses and lichens developed in the later period. The best-developed plant formation of the Oldest Dryas was sedge tundra with shrubs of dwarf willow and birch. This period ended about 12100 years ago in the area stretched between the minimum range of the Middle-Polish (Riss) Glaciation and the minimum range of the Baltic Glaciation (Witów near Łęczyca), and about 12500 years for the whole area of Poland (Książkiewicz et al., 1965; Wasylikowa, 1964; Woldstedt, 1958).

Only the species of moss mites that at the present time occur in the arctic region, tolerate continental climate, and can live in treeless areas could exist under the conditions of the Oldest Dryas. The species inhabiting mosses and lichens on a hard substratum should also be numbered in this category. Out of the forms that occur in the Poznań region today, the following species fulfill these conditions:

holo-Holarctic (Table X): *O. tibialis* (Nicolet) (161), *Z. exilis* (Nicolet) (162), *E. ribagai* Berlese (19),

Holarctic-Alpine (Table XI): *C. horrida* (Hermann) (26),

West Holarctic (Table XI): *C. labyrinthicus* (Michael) (80), *P. willmanni* van der Hammen (124),

Holarctic-subtropical (Table XII): *N. silvestris* Nicolet (23), *C. bipilis* (Hermann) (68), *T. sarekensis* Trägårdh (87),

semi-cosmopolitan (Table XIII): *O. nova* (Oudemans) (95), *P. peltifer* (C. L. Koch) (31).

All the moss mite species that were able to live in the Poznań region as early as the Oldest Dryas have wide ranges (Holarctic or wider). Some of them, showing a distinct association with forest environment in the area under study (e.g., *E. ribagai* Berlese), may have appeared as late as the Bölling interstadial. The moss mite fauna of the Oldest Dryas in the Poznań ragion probably included about 11 (6·2%) of the species living here now.

The Bölling interstadial dated back to the years 12500—12100 for the whole area of Poland and to the years 12275—11915 at Witów near Łęczyca (Wasylikowa, 1964). This was therefore a short period, lasting 350—400 years. The climate of the Bölling interstadial was far milder than that in the Oldest Dryas. The mean July temperature rose to about +15° C. The ice-sheet retreated to southern Sweden (to Skåne), the central portion of the Baltic Basin and Kurland, and a fresh-water reservoir was formed at its front edge. This must undoubtedly have moderated the continentality of the climate. Moreover, the Vistula had not its own estuary yet and flowed down along the „pradolina" of the Noteć and lower Warta. The presence of such a huge watercourse in the neighbourhood probably added to the decrease of continentality of the climate in the Poznań region. The general rule (Grichuk, 1961) that climate always become most continental towards the end of the glaciation and at the beginning of the interglacial was probably locally deranged in Wielkopolska.

The improvement of climate had an essential effect on the development of vegetation. We do not know so deep layers of deposits from the area under study as yet, but in Central Poland Bölling deposits containing remains of trees (birch and pine) have been uncovered. *Betula pubescens* Ehrh. and *Pinus silvestris* L. require a mean July temperature of about +12° C, but the birch spreads more rapidly. On account of the shortness of this period, the tree-form of birch probably dominated over the pine. Together with such shrubs as *Hippophae rhamnoides* L., *Betula sp.* and *Salix sp.*, they formed open scrubs of the nature of park-tundra. Large areas were still treeless, which is evidenced by pollen analyses showing a high share of *Artemisia* L., *Chenopodiaceae*, *Ephedra distachya* L. and others in the samples from the profiles examined (Książkiewicz et al., 1965; Tobolski, 1966, Wasylikowa, 1964).

The evident moderation of climate in the Bölling interstadial as compared with the Oldest Dryas and the appearance of trees enabled another group of species, unadapted to extreme continental climate but present in the arctic bioclimatic zone today to colonize the area examined. Ecologically we are probably concerned here with forms of open areas or those independent of plant cover and with different humidity requirements. These species may have been as follows:

North-European (Table V): *C. subarcticus* Trägårdh (84),

European-West Siberian (Table VI): *T. trimaculatus* (C. L. Koch) (138),

holo-Holarctic (Table X): *S. striculus* (C. L. Koch) (8), *T. tectorum* (Berlese) (32), *C. spinifer* (C. L. Koch) (27), *A. coleoptrata* (L.) (122), *O. unicarinata* (Paoli) (101), *O. ornata* (Oudemans) (96), *L. similis* (Michael) (169), *H. rufulus* C. L. Koch (1), *C. biurus* (C. L. Koch) (25), *H. paolianus longisetosus* Willmann (30), *B. lanceolata* (Michael) (106), *T. latirostris* (C. L. Koch) (131), *N. aurantiacus* (Oudemans) (154), *O. translamellata* (Willmann) (100),

West-Holarctic (Table XI): *P. punctata* (Nicolet) (123), *C. cuspidatus* (Michael) (146), *T. velatus* (Michael) (86), *H. thori* (Berlese) (29), *T. foveolatus* Willmann (38), *P. pilosus* Hammer (174), *A. latitecta* (Berlese) (126),

Holarctic-subtropical (Table XII): *Q. quadricarinata* (MICHAEL) (102), *R. ardua* (C. L. KOCH) (16), *N. anauniensis* CANESTRINI et FANZAGO (21), *S. pallidulus* (C. L. KOCH) (173).

In the Bölling interstadial the area under study may have been inhabited by about 28 species or 15·82% of the fauna examined (Table XXII); they are mostly the same geographical elements that began to appear in the Oldest Dryas. Towards the end of the Bölling interstadial in this area there probably lived all the West-Holarctic species present in the Poznań region now, all but one holo-Holarctic species, as well as most of the Holarctic-subtropical ones, and thus the species with the widest ranges still continued to appear in this area. It is naturally difficult to determine from which direction the migration proceeded in this case.

The Older Dryas was also a relatively short period (12100—11800). It is marked by an obvious deterioration of climate, which may be defined as arctic, cool and continental. The mean July temperature ranged from 10 to 12°C, and so its maximum values reached the minimum requirements of the birch and pine (KSIĄŻKIEWICZ et al., 1965; TOBOLSKI, 1966). At that time, according to FIRBAS (1949), in Central Europe, north of the Alps, there were solely different grass and shrub associations, the shrubs being represented by the dwarf birch and *Hippophae rhamnoides* L. The data obtained from the close environs of Poznań (OŁTUSZEWSKI, 1957) support this general picture entirely. *H. rhamnoides* L. and the dwarf willow and birch played the most important part in the area of the Wielkopolski National Park. A similar situation was also found in Central Poland (WASYLIKOWA, 1964; TOBOLSKI, 1966).

The deterioration of climate in respect of both temperature and humidity brought about the wane of trees in the study area and, as far as moss mites are concerned, the restoration of conditions that had occurred in the Oldest Dryas. In connection with this fact the extinction of the species that perhaps had occupied the environs of Poznań in the Bölling interstadial must be regarded as probable. If they survived this relatively short period of deterioration of the climate together with small clumps of *B. pubescens* EHRH. and *B. tortuosa* LODD. (= *B. carpatica* W. K.) subsisting at places (TOBOLSKI, 1966), this happened only quite locally.

The next period of the Late Glacial epoch was the Alleröd interstadial, which is relatively well known in any respect in the Polish territory. The obvious warming of climate caused the retreat of the icecap to the area of Central Swedish and Finnish moraines. The Alleröd, covering a small span of time (11800—11000), is noted for its fairly high climatic optimum. KSIĄŻKIEWICZ et al. (1965) characterize the climate of this period as cool-temperate, with the mean June temperature above +16°C. MARKOV et al. (1965) write that the mean annual temperature at a given place was 4°C higher in the Alleröd interstadial than in the Younger Dryas and the mean for July only 2° lower than nowadays.

Under these conditions most of Europe, both in the west (FIRBAS, 1949) and in the east (MARKOV et al., 1965), became covered by forests. In eastern Europe the northern boundary of the forest coincided with the present one, whereas the southern limits were shifted remarkably to the south (MARKOV et al., 1965). Most of the recently published papers concerning Poland emphasize the woody character of the Alleröd (TOBOLSKI, 1966 — see also for literature), but part of the authors claim that central and northern Poland was covered by sparse pine-birch forests, hardly better than park-tundra (DĄBROWSKI, 1959; OŁTUSZEWSKI, 1957; KSIĄŻKIEWICZ et al., 1965; SZAFER, 1952). However, an extremely interesting find of whole pine and birch trunks with crowns in the Mazurian Lake District (STASIAK, 1963), dated by the C^{14} method, proves that in the Alleröd interstadial the existence of closed forests was possible even in the north of Poland, at least at places. So far, no evidence (except for some pollen, probably brought by the wind) has been found for the existence of trees with higher thermic demands in Poland in the period discussed. Mammals were still represented by an arctic-tundra fauna with the species living in Arctic also at present.

It seems that not only the species that occurred in the Poznań region in the Bölling interstadial for the first time were able to recolonize this area in the Alleröd, but also a number of forest forms which now reach the boreal zone were present. The then quite evident presence of organogenic peat deposits indicates favourable living conditions also for typical peat-inhabitants. The sparse forests, at least locally, provided favourable conditions for species of open areas. In a relatively rich mosaic of environments the species living in mosses and lichens on a hard substratum found a suitable niche, as well. The following forms, in all probability, arrived in the area under discussion in the Alleröd interstadial:

holo-European (Table I): *A. pilosus* (C. L. KOCH) (73), *C. cymba* (NICOLET) (112), *L. licnophorus* (MICHAEL) (114), *M. pseudofusiger* (SCHWEIZER) (145),

West-European (Table II): *C. dentatus* (MICHAEL) (59), *P. lucorum* (C. L. KOCH) (166), *E. silvestris* (FORSSLUND) (65),

Central European (Table III): *L. ciliatus foveolatus* WILLMANN (110), *T. nigricans* WILLMANN (33), *M. italicus* (EYNDHOVEN) (62), *E. rauschenensis* (SELLNICK) (164), *C. tenuis* FORSSLUND (85),

East-European (Table V): *C. voigtsi* (OUDEMANS) (151), *C. spinosus* (SELLNICK) (150), *E. bituberculatus* (KULCZYŃSKI) (52), *C. minimus* SELLNICK (134),

South-East European (Table V): *P. sellnicki* (WILLMANN) (143),

North-European (Table V): *P. tardus* FORSSLUND (14),

European-West Siberian (Table VI): *T. incisellus* (KRAMER) (139), *P. phaenotus* (C. L. KOCH) (121), *E. occultus* (C. L. KOCH) (119), *T. carinatus* (C. L. KOCH) (3), *L. coracinus* (C. L. KOCH) (69), *E. acromios* (HERMANN) (115), *C. femoralis rugosior* (BERLESE) (79), *M. brevipes* (MICHAEL) (113), *H. gilvipes* (C. L. KOCH) (76), *O. bicarinata* (PAOLI) (89), *O. fallax obsoleta* (PAOLI) (90), *O. pectinata*

(MICHAEL) (107), *O. paolii* (OUDEMANS) (108), *E. duplex* BERLESE) (116), *C. sellnicki* RAJSKI (135), *E. kamaensis* (SELLNICK) (53), *A. tragardhi* FORSSLUND (104),

European-Middle Asiatic (Table VII): *P. hexagonus* BERLESE (142),

European-Siberian (Table VII): *N. palustris* C. L. KOCH (20), *P. spinosa* (SELLNICK) (56),

European-Manchurian (Table VII): *D. (P.) clavipes* (HERMANN) (48), *G. fusifer* (C. L. KOCH) (60), *X. badensis* (SELLNICK) (175),

temperate-holo-Holarctic (Table VIII): *A. longilamellata* (MICHAEL) (103), *G. bicostatus* (C. L. KOCH) (46), *P. piger* (SCOPOLI) (13), *S. latipes* (C. L. KOCH) (171), *P. punctum* (C. L. KOCH) (141), *O. subpectinata* (OUDEMANS) (99), *O. minus* (PAOLI) (93), *P. tenuiclava* (BERLESE) (159), *C. cepheiformis* (NICOLET) (58), *N. coronata* BERLESE (41), *C. latus* C. L. KOCH (57), *E. cribrarius* (BERLESE) (15), *F. fuscipes* (C. L. KOCH) (136), *P. italicus* (OUDEMANS) (10),

western temperate-Holarctic (Table IX): *A. ovatus* (C. L. KOCH) (70), *C. coriaceus* (C. L. KOCH) (76), *O. calcarata* (C. L. KOCH) (127), *A. longipluma* (BERLESE) (160), *P. globosus* (C. L. KOCH) (9), *C. borealis* (TRÄGÅRDH) (147), *P. ligneus* WILLMANN (12), *N. nanus* (NICOLET) (39), *T. glaber* (MICHAEL) (37), *C. minusculus* BERLESE (82), *T. novus* (SELLNICK) (140), *L. humerata* SELLNICK (170), *P. bella* (SELLNICK) (125), *C. areolatus* BERLESE (77), *M. gracilis* VAN der HAMMEN (35),

holo-Holarctic (Table X): *N. pratensis* SELLNICK (22),

subbipolar (Table XII): *C. gracilis* (MICHAEL) (132), *G. elimata* (C. L. KOCH) (156), *P. nervosa* (BERLESE) (158),

Holarctic-subtropical (Table XII): *E. minutissimus* (BERLESE) (2),

temperate-Holarctic-tropical (Table XIII): *S. laevigetus* (C. L. KOCH) (172), *C. segnis* (HERMANN) (24), *X. capucinus* (BERLESE) (176),

semi-cosmopolitan (Table XIII): *T. excavatus* (WILLMAN) (34), *T. novus* (SELLNICK) (36), *H. initialis* (BERLESE) (168), *F. quadripertitus* GRANDJEAN) 67).

It may well be that the moss mite fauna of the Poznań region was still richer in the Alleröd interstadial and contained also a number of forms now rather associated with deciduous forests or not going beyond the temperate bioclimatic zone in the north of the range, which is indicated by the finding of three species, *S. applicatus* (SELLNICK) (4), *T. novus* (SELLNICK) (36) and *L. rugosus* (SELLNICK) (111), in a gyttja dated back to the Alleröd in Denmark (SØGAARD, 1938). I have referred only the appearance of the second of them in the area examined to the Alleröd interstadial on the basis of the data in my possession. To be sure, *S. applicatus* (SELLNICK) occurs in the boreal bioclimatic zone today, but it is as a rule associated with deciduous forests (Table I), whereas *L. rugosus* (SELLNICK) has been recorded exclusively from the temperate bioclimatic zone today (Table II). In accordance with the method adopted here one would expect the appearance of these two species in the Poznań region as late as the Holocene.

The relatively mild climate of the Alleröd interstadial contributed not only to the considerable increase in the number of species in the study area, but also to the enrichment of the fauna in new geographical elements (Table XXII). Including the forms which had come and settled down here in the previous periods, the moss mite fauna numbered, probably as early as then, about 120 species, i.e., 68·93% of the present-day fauna. Nearly all the geographical elements living here today were already represented, the appearance of temperate-Holarctic and Palaearctic species for the first time in the late glacial period, and, what is more, in large numbers, being characteristic of the Alleröd interstadial. This is especially true — out of these last species — of the European-Manchurian and European-West Siberian groups. A certain number of the European species, except for the South European, also appeared then for the first time. The kind of the geographical elements that appeared may be an indication as to the direction of their migrations, especially in the case of the West- or East-European species.

The last period of the Neopleistocene, the Younger Dryas, fell in the years 11000 to 10100, i.e., the time when the ice-sheet stopped in the area of the Fennoscandian moraines. It was a period of definite deterioration of the climate, which was again continental in character, and the mean July temperature dropped to about +12°C in the region examined, that is to say, it maintained at the lowest value allowing the vegetation of the birch and pine. However, these species were remarkably restricted, more in the west of Poland than in its central and eastern parts, it seems. In the Wielkopolski National Park Ołtuszewski (1957) found an exclusive occurrence of woodless tundra with *Hippophae rhamnoides* L. and willow in the Younger Dryas. Tobolski (1966) holds the opinion that in spite of the dominance of steppe species, *Pinus silvestris* L. and *Betula verrucosa* Ehrh. were able to persist as species. On the other hand, Wasylikowa (1964) and Dąbrowski (1959) have proved the existence of pine forests, however sparse they were, in the Younger Dryas of central and eastern Poland. Firbas (1949), Książkiewicz et al. (1965) and Szafer (1952) write about the wane of forests in nearly whole Poland.

It is obvious that under such conditions no new species could have arrived in this region. The only change that might be expected was probably a marked restriction of the occurrence of the forms which had appeared in the Poznań region during the Alleröd interstadial. It may well be that some of them disappeared completely and others managed to subsist locally together with the stands of pine forests, varying in area. Since in the Poznań region there are no peat deposits containing the Younger Dryas horizon (Szafer, 1952), the possibility of extinction of peat-inhabitants in this area cannot be excluded. In all probability, the confinement of wooded areas caused also the extinction of the species which now reach only the boreal bioclimatic zone in the north and occur, above all, in forests. These were most likely the following forms:

holo-European (Table I): *S. applicatus* (Sellnick) (4), *L. licnophorus* (Michael) (114),

West-European (Table II): *C. dentatus* (MICHAEL) (59), *E. silvestris* (FORSSLUND) (65), *L. rugosus* (SELLNICK) (111),

Central European (Table III): *L. ciliatus foveolatus* WILLMANN (110), *T. nigricans* WILLMANN (33), *M. italicus* (EYNDHOVEN) (62),

East-European (Table V): *C. voigtsi* (OUDEMANS) (151), *C. minimus* SELLNICK (134), *P. tardus* FORSSLUND (14),

European-West Siberian (Table VI): *C. femoralis rugosior* BERLESE (79), *H. gilvipes* (C. L. KOCH) (75), *O. bicarinata* (PAOLI) (89), *E. duplex* (BERLESE) (116), *A. tragardhi* FORSSLUND (104),

European-Siberian (Table VII): *P. spinosa* (SELLNICK) (56),

European-Manchurian (Table VII): *D. (P.) clavipes* (HERMANN) (48),

temperate-Holarctic (Table VIII): *A. longilamellata* (MICHAEL) (103), *P. piger* (SCOPOLI) (13), *O. minus* (PAOLI) (93), *P. tenuiclava* (BERLESE) (159), *C. cepheiformis* (NICOLET) (58), *N. coronata* BERLESE (41), *C. latus* C. L. KOCH (57), *E. cribrarius* (BERLESE) (15), *P. italicus* (OUDEMANS) (10),

western temperate-Holarctic (Table IX): *A. ovatus* (C. L. KOCH) (70), *C. coriaceus* (C. L. KOCH) (76), *O. calcarata* (C. L. KOCH) (127), *A. longipluma* (BERLESE) (160), *P. globosus* (C. L. KOCH) (9), *C. borealis* (TRÄGÅRDH) (147), *P. ligneus* WILLMANN (12), *C. areolatus* BERLESE (77),

semi-cosmopolitan (Table XIII): *T. excavatus* (WILLMANN) (34), *T. novus* (SELLNICK) (36).

To sum up, the moss mite fauna of the Poznań region impoverished probably by 37 species in the Younger Dryas (Table XXII), the European and temperate-Holarctic species and to a smaller extent the Palaearctic ones being chiefly those on the wane. The holo-Holarctic species and the widely distributed forms underwent hardly any changes.

Towards the end of the Pleistocene about 85 species (for matter-of-course reasons I leave out the species which are boreal or arctic now and probably occurred in the study area in different periods of the late glaciation) lived in the region examined and formed 48·03 % of the present-day fauna. Particularly well represented species were the North-European (100 % of the modern species), European-West Siberian (somewhat above 50 %), temperate-holo-Holarctic (about 33 %), holo-Holarctic (100 %) and most of the widely distributed species. The European and Palaearctic species and a considerable portion of the temperate-Holarctic ones did not occupy the study area permanently yet.

The Holocene, like the late Neopleistocene, may be divided into five periods: Preboreal, Boreal, Atlantic, Subboreal and Subatlantic.

In the Preboreal period (10100—9500) the climate improved evidently as compared with that of the Younger Dryas, but it was not as mild as in the Alleröd interstadial. KSIĄŻKIEWICZ and his collaborators (1965) define it as fairly warm, though the mean July temperature fluctuated between 14 and 15° C. According to WALTER (1954), the climate of the Preboreal was relatively dry, like that in the Upper Neopleistocene, and in this it differed from the next phases of the Holocene.

The northern boundary of the Preboreal forests of Central Europe ran most likely at the same geographical latitude as it does today, and the forests were already closed ones, though, presumably, steppe formations (*Artemisia* L.) dominated in areas which now have the rainfall lower than 500 mm per year. The forests were composed of the birch and pine in varying proportions (Firbas, 1949). In Wielkopolska the proportion of the pine increased in the Preboreal from the value reached in the Younger Dryas (25%) to the absolutely highest values (75%), characteristic of the Alleröd interstadial and the Boreal period (Walter, 1954). Species with higher thermal requirements, such as the hornbeam, elm, linden and hazel, appeared in the Białowieża National Park towards the end of the Preboreal (Dąbrowski, 1959). In spite of the great continentality of climate, peat-bogs began to form in the Preboreal period (Książkiewicz et al., 1965). At that time pine-birch forests with a small admixture of willow dominated in the close environs of Poznań (Ołtuszewski, 1957). A slight dominance of the pine was observed only exceptionally. In general, both forest-building species were in perfect equilibrium. Ołtuszewski (l. c.) found no thermophilous forms. According to Tobolski (1966), a general regularity of this period was the dominance of the pine over the birch (*B. verrucosa* Ehrh.) in dune areas.

Under such conditions the study area could be recolonized merely by the species that had existed in it in the Alleröd interstadial and had undergone extinction or at least heavy restriction in the Younger Dryas (Table XXII). The foregoing concerns both peat-inhabitants and forest species. The arrival of more thermophilous species in the Poznań region in the Preboreal seems improbable.

Unlike the series of the relatively short preceding periods, the Boreal lasted for about 3000 years (9500—6500), during which the climate became gradually milder and more humid. Thus, the period of continental climate, which dominated more or less markedly from the retreat of the ice to the end of the Preboreal, was ended. Dąbrowski (1959) established on the basis of the presence of *Hedera helix* L. in the Białowieża National Park that the minimum mean temperature of the coldest month was $-2°C$ and that of the warmest month at least $+13°C$. In the opinion of Książkiewicz and his collaborators (1965), the mean temperatures of the Boreal period were higher than at present and the climate approximated to the Holocene optimum.

All the authors emphasize in concert the dominance of the pine over the birch in the Boreal of Central Europe. The pine attained also its Holocene maximum in Wielkopolska (Walter, 1954). Thermophilous species began to appear beside the pine in the territory of Poland, e.g., the elm, linden, oak, hornbeam and hazel in the Białowieża National Park (Dąbrowski, 1959), the first two species being dominant even in mixed forests. In the catchment basin of the Prosna, and so at a far shorter distance from the study area, there occur birches, elms and hazels in small numbers in the pine-dominated forests (Tobolski, 1966). In the area of the Wielkopolski National Park (Ołtuszewski,

1957) the pine reached its Holocene maximum and the hazel the postglacial maximum, whereas the following genera appeared as forest components: *Ulmus* L. (4%), *Quercus* L. (5%), *Tilia* L. (2%) and *Alnus* Mill. (15%), without however forming deciduous or even mixed forests.

Not only the species of coniferous forests, but also mesohygrs, typical of deciduous forests, could occur in such environments in Wielkopolska. As, according to Czubiński (1950), the forests of that period were open to the extent that they did not inhibit the migrations of heliophilous forms, the thermophilous species, living also in the south-eastern European steppes, most likely reached the Poznań region in the Boreal period, as well. These forms were as follows:

holo-European (Table I): *C. marginatus* (Michael) (81), *C. subglobulus* (Oudemans) (152), *C. femoralis* (Nicolet) (78), *O. quadrimaculata* Evans (97), *G. lanceata* (Oudemans) (157),

West-European (Table II): *R. duplicata* (Grandjean) (17), *X. permixtus* (André) (72),

Central European (Table III): *A. willmanni* (Dyrdowska) (105), *O. tecta* (Michael) (130),

South-European (Table IV): *H. dolosa* Grandjean (43), *H. punctulata* Berlese (44), *H. punctulata septentrionalis* Berlese (45), *M. pulverosa* Strenzke (55), *O. meridionalis* Berlese (128), *O. reticulata* Berlese (129), *E. hirtus* (Berlese) (117), *D. plantivaga* (Berlese) (167),

South-East European (Table V): *Z. propinquus* (Oudemans) (163), *A. polonicus* Kulczyński (66), *O. furcata* (Willmann) (92),

European-West Siberian (Table VI): *E. tardus* (C. L. Koch) (120) *D. (H.) riparius* Nicolet (49), *D. (S.) subverticillipes* Bulanova-Zakhvatkina (51),

European-Manchurian (Table VII): *X. clypeator* Robineau-Desvoidy (71), *H. targionii* (Berlese) (28), *C. pusillus* (Berlese) (148), *C. falcata* Evans (74),

temperate-holo-Holarctic (Table VIII): *M. minima* (Berlese) (18),

western temperate-Holarctic (Table IX): *M. papillipes* (Nicolet) (54), *N. elegantula* Berlese (42).

An evident increase in the number of species with less extensive ranges, especially the European species with the exception of the West-European ones, can be observed in the Boreal period (Table XXII). The settlement of a large number of South-European and South-East European species (in relation to those living in this area at present) is a particularly striking phenomenon. A noteworthy fact is also the appearance of more than the half of all the European-Manchurian species. Altogether, 30 species or 17% of the fauna examined settled down in the Poznań region in the Boreal period. The total of species living in this area at the end of the Boreal was approximately 152, which is nearly 86% of the modern fauna.

The last major wave of migrations reached the Poznań region in the Atlantic period (6500—4000), which lasted for 2500 years, only somewhat shorter than the Boreal. The climate was still changing to the effect that the means of both

temperature and humidity rose. As a result, the Atlantic period is also defined as the climatic optimum of the Holocene (Książkiewicz et al., 1965) and its climate as having characters of the Atlantic (oceanic) climate. A fairly clear-cut boundary between the western area of deciduous forests and the eastern area of coniferous forests developed in Central Europe in the Atlantic, the belt of the Middle Polish Lowlands being included in the latter. In the Poznań region the pine pollen forms 50—70% of the total tree pollen, whereas the oak and linden pollen does not exceed 10%. The deciduous trees probably won a dominant position on clayey soilds and the original steppes vanished completely (Firbas, 1949; Walter, 1954). In the area of the Białowieża National Park the deciduous forests, in which the hornbeam was of fundamental importance and the oak came in second, attained the Holocene maximum. The proportions of the elm and linden had not changed significantly since the Boreal. A growth of mesophilous deciduous forests, composed of the oak, maple, ash, and hazel, was found also in the Prosna valley (Tobolski, 1966). The maximum development of oak-dominated mixed forests in the Holocene took place in the area of the Wielkopolski National Park (Ołtuszewski, 1957). The elm and linden, as components of these forests, reached their postglacial maxima, and the pine its minimum. In the second half of the Atlantic period the proportions of the elm and linden decreased in the oak forests, whereas the values for the alder were very high. The hornbeam and beech appeared in small proportions (1—2%). Thus, in the close environs of Poznań the mesophilous and even hygrophilous deciduous forests rose somewhat in importance in spite of the still subsisting high proportion of the pine.

The development of the moss mite fauna probably tended towards the permanent settlement of the forest mesohygrs and the expansion of their ranges. Their first representatives appeared in the Poznań region during the Boreal. On the other hand, the Atlantic period very likely provided favourable conditions also for the influx of hygrophilous forest species and those associated with the suboceanic climate. The following species of the present-day fauna should be mentioned here:

holo-European (Table I): *M. semirufus* (C. L. Koch) (144), *E. globulus* (Nicolet) (153), *D. (D.) onustus* C. L. Koch (47),

West-European (Table II): *N. comitalis* Berlese (40), *E. hepaticus* C. L. Koch (63), *T. cuspidentatus* Knülle (88), *G. alata* (Hermann) (155), *E. oblongus* (C. L. Koch) (64), *H. thienemanni* Strenzke (109), *C. schutzi* (Oudemans) (149),

Central European (Table III): *D. (S.) boreus* Bulanova-Zakhvatkina (50), *O. falcata marginedentata* Strenzke (91), *O. sigma conjuncta* Strenzke (98), *E. hygrophilus* (Knülle) (118), *S. spinosus* (Sellnick) (7), *E. gessneri* Willmann (165),

South-European (Table IV): *P. lentulus* (C. L. Koch) (11), *Z. micronychus* (Berlese) (61), *S. laevigatus* (C. L. Koch) (5),

East-European (Table V): *X. variabilis* (Rajski) (177),

European-West Siberian (Table VI): *O. neerlandica* (Oudemans) (94),

western temperate-Holarctic (Table IX): *S. magnus* (Nicolet) (6), *C. mediocris* Berlese (135).

A tendency for the European species, mostly West- and Central European ones, to colonize the study area persisted in the Atlantic period (Table XXII). Out of the 23 species that, in all probability, appeared in the Atlantic period, 13 were West- and Central European. Presumably, all the species inhabiting the Poznań region today were already there towards the end of the Atlantic period (Table XXII).

A general survey of Table XXII shows that an essential turn in the development of the moss mite fauna of the Poznań region took place in the Alleröd interstadial, when in the area examined there were already representatives of all the geographical elements that occur in it today and nearly 69% of the species except for the South-European species. True enough, in the Younger Dryas a great part (37) of the species, unable to stand the severe climate of this period, perished or became remarkably limited, but some representatives of most of the geographical elements probably succeeded in persisting. A characteristic of the development of this fauna in the Holocene is the continuation of the developmental tendency originating in the Alleröd, only that the species which settled down in particular periods had different ecological requirements; nevertheless they were always, above all, European and Palaearctic species. As for the Holarctic forms, there is a great probability that they also persisted locally in the study area in the Younger Dryas.

A cooling of climate combined with a further increase in humidity occurred in the terminal periods of the Holocene, i.e., in the Subboreal (4000—2500) and Subatlantic (from 2500 up to the Present) (Książkiewicz et al., 1965). In the Subboreal period these changes were accompanied by the expansion of the beech and, to a smaller extent, that of the fir and hornbeam in whole Central Europe, north of the Alps. This led to a relatively stabilized situation in the Subatlantic period, marked by the dominance of the beech and fir over large areas. Successive immigrations of different floral elements, preceding that period, brought about a remarkable differentiation of plant associations according to the edaphic and climatic local conditions.

The results obtained from a pollen analysis, which in this case somewhat distorts the actual situation, show that the pine was still the dominant forest-building species in Wielkopolska, accompanied by the oak, occurring however in small proportions, under any edaphic conditions. The beech was also present, but largely scattered, all over the area (Firbas, 1949). In the area of the Wielkopolski National Park the Subboreal period is weakly signalized by a rise in the pollen curves for the pine, hazel, and hornbeam, and the Subatlantic period by an increase in the proportions of the hornbeam, beech (about 3% of the stand) and alder. The pine however still remained the dominant forest-building species (Ołtuszewski, 1957).

The influence of human settlement appeared in the Subboreal and Subatlantic periods and was combined with a reduction in the wooded area,

especially on fertile soils in the valleys of small rivers (TOBOLSKI, 1966). This was connected with the limitation of areas covered by deciduous forests in favour of meadow and steppe associations (cultivated areas). In the last thousand years the area of forests decreased considerably (to about 25%) and the proportion of the pine, as the source of the timber most in demand, increased in them (WALTER, 1954).

It is quite probable that some West-European species of moss mites and some other hygrophilous forms, whose arrival in the study area I have referred to the Atlantic period, reached the Poznań region as late as the Subboreal. The essential changes that took place in the moss mite fauna of this area in the period discussed were however most likely chiefly quantitative in nature. Along with the reduction of the wooded areas, the general area accessible for these animals decreased, and it may well be that part of them perished completely. On the other hand the mesophilous and hygrophilous species independent of plant cover (RAJSKI, 1961, Table X) have more and more increased both in their ranges and in abundance in connection with the development of meadows and pastures.

As I have already emphasized at the beginning of this section, each reconstruction contains some hypothetical elements and therefore is expected to be modified in the course of further study. The present state of knowledge of the ecology of moss mites and the development of their habitats in the postglacial period, as well as the lack of adequate fossil materials suggest that the reconstruction presented in this paper also describes the actual situation only with approximation.

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STRESZCZENIE

Niniejsza praca jest trzecią częścią cyklu, poświęconego autekologii i zoogeografii fauny mechowców okolic Poznania i zawiera analizę zoogeograficzną.

1. Wyróżniono 21 grup gatunków, o różnych zasięgach geograficznych (tab. XIV). Dla każdego gatunku podano definicję areału oraz charakterystyczne jego cechy: przebieg granic zasięgów przez Polskę, dysjunkcje i typowe obszary ostojowe. Poszczególne gatunki określono również pod względem ekologicznym. Definicje zasięgów sporządzono metodą Meusela et al. (1965), która pozwala określić indywidualnie stosunek zasięgu każdego gatunku do stref temperatury makroklimatu, stref klimatyczno-roślinnych w górach, wilgotności makroklimatu, oraz opisać rozmieszczenie gatunku na poszczególnych kontynentach (tab. I—XIII).

Okazało się, że badana fauna jest mało specyficzna. Gatunków o zasięgach europejskich jest tylko 35%. Dominują zaś gatunki o zasięgach większych niż europejskie (65%). Na uwagę zasługuje również mały udział (7,35%) gatunków środkowoeuropejskich, które można by uznać za endemiczne. Wśród gatunków, których zasięgi są ukierunkowane w stosunku do okolic Poznania (tab. XV), przeważają gatunki południowe (10,16%) i zachodnie (7,35%), nad północnymi (4,52%), wschodnimi i południowo-wschodnimi (po 2,82%).

2. Zbadanie stosunku ekoelementów do geoelementów (tab. XVI) pozwoliło ustalić dla badanej fauny następujące prawidłowości: Typowym elementem ekologicznym geoelementu europejskiego są gatunki lasów liściastych i gatunki kserofilne, żyjące w środowisku roślin zarodnikowych na twardym podłożu. Typowym elementem ekologicznym geoelementu holarktycznego są niespecyficzne gatunki leśne, gatunki lasów iglastych i tyrfobionty. Typowym elementem ekologicznym wśród gatunków szeroko rozsiedlonych są formy niezależne od szaty roślinnej.

3. Przedmiotem analizy stała się również zależność fauny mechowców okolic Poznania od wilgotności makroklimatu (tab. XVII). Okazało się, że większość gatunków (69,49%) jest stosunkowo niezależna od wilgotności makroklimatu i występuje w strefach oceanicznej, suboceanicznej i subkontynentalnej. 12,43% gatunków stwierdzono ponadto także na obszarach o klimacie kontynentalnym. Na gatunki ograniczone tylko do dwu stref: oceanicznej i suboceanicznej albo suboceanicznej i subkontynentalnej przypada po 6,78%. Wreszcie tylko 4,52% stanowią gatunki występujące wyłącznie w typowej dla badanego obszaru strefie suboceanicznej.

4. Na przykładzie fauny mechowców okolic Poznania zbadano prawidłowość M. Hammer (1962), mówiącą, że fauna mechowców wilgotnych biotopów ma bardziej kosmopolityczny charakter niż fauna kserofilna (tab. XVIII). Okazało się, że wspomnianą prawidłowość należy rozumieć w ten sposób, że wśród oligohygrów (gatunki o niskich wymaganiach w stosunku do wilgotności) istnieje mniej gatunków, stosunkowo szeroko rozsiedlonych, niż wśród mezo- i polihygrów łącznie.

5. Na podstawie struktury współczesnych zasięgów (dysjunkcje i obszary ostojowe) i w pewnej mierze na podstawie materiałów paleontologicznych (mechowce z bursztynu), starano się ustalić najstarsze fragmenty zasięgów i w ten sposób określić minimalny, bezwzględny wiek badanych gatunków. Podstawą tych rozważań stały się następujące twierdzenia i fakty: mechowce (a także niektóre inne zwierzęta) występują na ogół w związku z określonym typem roślinności, reprezentującym zwykle wyższą jednostkę fitosocjologiczną (rząd etc.) lub będącym wprost określoną formacją roślinną; zgodnie z osiągniętymi dotąd wynikami, bierne przenoszenie się mechowców w skali międzykontynentalnej jest mało prawdopodobne; gatunki zwierzęce, a w szczególności mechowce, odznaczają się stałością wymagań ekologicznych w ciągu całego okresu istnienia; politopowe powstawanie gatunków jest (szczególnie w świecie zwierzęcym) rzadkością, nie odgrywającą poważniejszej roli wśród organizmów żywych; analiza współczesnych zasięgów roślin czy zwierząt nie upoważnia do wnioskowania o historii ich kształtowania się, sięgającego w przeszłość starszą od paleogenu; powierzchnia kontynentów i oceanów kształtowała się zgodnie z teorią Wegenera. Opierając się na rekonstrukcjach paleogeograficznych i przedstawionych wyżej twierdzeniach i faktach, przeanalizowano zasięgi wszystkich badanych gatunków.

Występowanie w bursztynie bałtyckim, dysjunkcja między Europą i Krainą Orientalną u niezależnych od temperatury polihygrów, reliktowe występowanie na Maderze, w Kolchidzie i na Nizinie Lenkorańskiej, wreszcie dysjunkcja południowopacyficzna świadczą o paleogeńskim pochodzeniu fragmentów zasięgów 20 gatunków, tj. 11,30% badanej fauny.

Istnienie i zanik połączeń lądowych między Azją i Ameryką Północną oraz Europą i Ameryką Północną oraz możliwość migracji przez te połączenia gatunków, o określonych wymaganiach ekologicznych; powstanie tzw. dysjunkcji europejsko-mandżurskiej w zasięgu lasów liściastych i związanych z nimi gatunków zwierząt; wreszcie reliktowe stanowiska określonych gatunków w typowych ostojach fauny trzeciorzędowej: na Maderze, Sardynii i Korsyce, w Kolchidzie, na Nizinie Lenkorańskiej i w niektórych partiach lasów liściastych w Azji, uważanych za resztki lasów turgajskich, pozwoliło stwierdzić, że najstarsze partie zasięgów 77 gatunków (tab. XIX), tj. 43,50% badanej fauny, kształtowały się w neogenie.

Możliwość migracji przez obszar beryngijski w glacjałach, przez obszar dysjunkcji europejsko-mandżurskiej w interglacjale eemskim, istnienie dysjunkcji holarktyczno-andyjskiej i niektóre inne cechy zasięgów świadczą, że w 47 przypadkach badane areały powstały częściowo w czwartorzędzie. Jednakże tylko u 20 gatunków, tj. u 11,30% badanej fauny, zasięgi mają wyłącznie cechy czwartorzędowe (tab. XX).

W przypadku 60 gatunków (33,90%) nie udało się ustalić charakterystycznych, dających się powiązać z określonym momentem historycznym, cech zasięgów (tab. XXI).

6. Stosunkowo dobra znajomość rozwoju środowiska geograficznego i ro-

ślinności okolic Poznania w postglacjale oraz wymagań ekologicznych mechowców, zarówno w stosunku do mikro-, jak i makroklimatu, pozwoliła sformułować hipotezę o rozwoju fauny mechowców okolic Poznania w ciągu ostatnich kilkunastu tysięcy lat (tab. XXII i XXIII). Dotyczy ona tylko gatunków występujących współcześnie na badanym terenie i w znacznym skrócie przedstawia się następująco:

W warunkach najstarszego dryasu mogły występować w okolicach Poznania jedynie te gatunki mechowców, które są współcześnie reprezentowane w obszarze arktycznym, znoszą klimat kontynentalny i mogą żyć w terenie nie pokrytym roślinnością drzewiastą, w szczególności lasami, oraz gatunki, występujące wśród roślin zarodnikowych na twardym podłożu. 11 gatunków (6,2%) spośród współczesnej fauny spełnia te warunki. Wszystkie mają zasięgi holarktyczne lub większe.

W interstadiale Bölling osiedliły się na badanym terenie prawdopodobnie gatunki, nie przystosowane do klimatu skrajnie kontynentalnego, ale występujące współcześnie w bioklimatycznej strefie arktycznej. Pod względem ekologicznym są to formy terenów otwartych lub niezależne od roślinności, o różnych wymaganiach wilgotności. Takich gatunków jest w badanej faunie 28 czyli 15,82%. Wszystkie mają bardzo duże zasięgi. Gatunki te zaniknęły w Wielkopolsce lub przynajmniej zostały poważnie ograniczone w starszym dryasie, kiedy klimat uległ znacznemu pogorszeniu.

Prawdziwy przełom w rozwoju fauny mechowców okolic Poznania nastąpił prawdopodobnie w interstadiale Alleröd, kiedy zaistniały warunki osiedlenia się form leśnych, tyrfobiontów, form światłolubnych i związanych ze środowiskiem roślin niższych na twardym podłożu, sięgających współcześnie na północy tylko do bioklimatycznej strefy borealnej. Razem z formami, które dotarły i osiedliły się tu w poprzednich okresach, fauna mechowców liczyła prawdopodobnie już wówczas około 120 gatunków, tj. 68,93% fauny współczesnej. Cechą charakterystyczną tego okresu jest pojawienie się dużej liczby gatunków umiarkowanoholarktycznych i palearktycznych oraz pewnej liczby gatunków europejskich z wyjątkiem południowoeuropejskich.

Drugi regres w rozwoju badanej fauny nastąpił w młodszym dryasie, w związku z ponownym pogorszeniem się klimatu. Zanikowi uległo prawdopodobnie 37 gatunków, głównie leśnych, o zasięgach europejskich i umiarkowanoholarktycznych. Powróciły one na badany teren być może już w okresie preborealnym.

W okresie borealnym mogły już występować w Wielkopolsce europejskie (z wyjątkiem zachodnioeuropejskich) i europejsko-mandżurskie mezohygry, typowe dla lasów liściastych oraz gatunki ciepłolubne, pochodzenia południowo-wschodnio-europejskiego. Badana fauna wzbogaciła się wówczas prawdopodobnie o 30 gatunków, tj. 17% fauny współczesnej i liczyła już, być może, 152 gatunki, tj. 86% znanych tu obecnie.

Pozostałe 14% gatunków, głównie zachodnio- i środkowoeuropejskich, pojawiło się prawdopodobnie w okolicach Poznania w okresie atlantyckim, przy

czym były to przeważnie leśne mezo- i polihygry oraz inne formy, związane współcześnie z klimatem suboceanicznym.

W okresie subborealnym i subatlantyckim zachodziły w badanej faunie przypuszczalnie tylko zmiany ilościowe, w związku ze zmniejszaniem się powierzchni lasów pod wpływem osadnictwa.

Stwierdzone fakty i przedstawione hipotezy w miarę możności zinterpretowano i przedyskutowano krytycznie.

РЕЗЮМЕ

Настоящая работа является третьей частью цикла, посвящённого аутэкологии и зоогеографии фауны панцирных клещей окрестностей Познани и содержит зоогеографический анализ.

1. Выделено 21 группу видов об различных географических областях распространения (табл. XIV). Для каждого вида дано определение ареала и характерные его признаки: прохождение границ областей распространения через Польшу, дизъюнкции и типичные приютные территории. Отдельные виды определено в экологическом отношении. Определения областей распространения составлено по методу Meusel и др. (1965), который позволяет определить индивидуально отношение области распространения каждого вида к зонам температуры макроклимата, климатическо-растительным зонам в горах, влаги макроклимата, а также описать размещение вида на отдельных континентах (табл. I—XIII).

Оказалось, что исследованная фауна мало специфическая. Видов, которые имеют европейские области распространения только 35%. Доминируют виды, которых области распространения больше чем европейские (65%). Заслуживает внимания незначительное участие (7,35%) среднеевропейских видов, которые можно было бы признать за эндемические. Среди видов, которых области распространения направлены к окрестностям Познани (табл. XV), превалируют южные виды (10,16%) и западные (7,35%), над северными (4,52%), восточными и юго-восточными (по 2,82%).

2. Изучение соотношения экоэлементов к геоэлементам (табл. XVI) позволило установить для исследуемой фауны следующие закономерности: типичным экологическим элементом европейского геоэлемента являются виды лиственных лесов и ксерофильные виды, обитающие в среде споровых растений на твёрдом субстрате. Типичным экологическим элементом голарктического геоэлемента являются неспецифические лесные виды, виды хвойных лесов и тырфобионты. Типичным экологическим элементом среди широко расселённых видов являются формы независимые от растительного покрова.

3. Предметом анализа была также зависимость фауны панцирных клещей окрестностей Познани от влажности макроклимата (табл. XVII). Оказалось, что большинство видов (69,49%) является относительно независимыми от влаги микроклимата и появляется в океанской, субокеанской и субконтинентальной зонах. 12,43% видов, кроме этого, найдено также там, где преобладает континентальный климат. На виды ограниченные лишь к двум зонам: океанской и субокеанской или субокеанской и субконтинентальной приходится по 6,78%. Наконец, лишь 4,52% составляют виды, распорстранённые в типичной для исследованной местности субокеанской зоне.

4. На примере фауны панцирных клещей окрестностей Познани исследовано закономерность Hammer (1962), утверждающую, что фауна панцирных клещей влажных биотопов имеет более космополитический характер чем ксерофильная фауна (табл. XVIII). Оказывается, упомянутую закономерность следует понимать так что среди олигогигров (виды, требующие незначительное количество влаги) существует меньше видов относительно широко расселённых, чем среди мезо и полигигров вместе взятых.

5. На основании структуры современных областей распространения (дизъюнкци и приютные пространства), а также в некоторой степени на основании палеонтологических материалов (панцирные клещи из янтаря) мы пытались установить старейшие фрагменты областей распространения и таким образом определить минимальный, безусловный возраст исследуемых видов. Основанием этих рассуждений стали следующие рассуждения и факты: панцирные клещи (а также некоторые другие животные) в общем обитают в связи с определённым типом растительности обычно представляющим высшую фитосоциологическую еденицу (отряд и.т.д.) или будучи прямо определённой растительной формацией; согласно полученным до сих пор результатам пассивное перемещение панцирных клещей в межконтинентальном масштабе является мало вероятным; виды животных, а в особенности панцирные клещи, отличаются постоянством экологических требований в течении всего периода существования. Политоповое возникновение видов является (особенно в мире животных) редкостью, не имеющей важного значения среди живых организмов; анализ современных областей распространения растений или животных не даёт основания к заключению об их истории возникновения, в прошлом, старшем палеогенового периода; поверхность континентов и океанов образовалась согласно теории Вегенера. Опираясь на палеогеографические реконструкции, а также представленные положения и факты, проанализировано области распространения всех исследованных видов.

Наличие в Балтийском янтаре, дизъюнкция между Европой и Орьентальной областью у независимых от температуры полигигров, реликтовое присутствие на Мадейре, Колхиде и Ленкоранской низменности, наконец дизъюнкция южной части Тихого океана свидетельствуют о палеогенном происхождении фрагментов областей распространения 20 видов, то есть 11,30% исследованной фауны.

Существование и исчезновение материковых связей между Азией и Сев. Америкой, а также между Европой и Сев. Америкой и возможность миграции видов с определе́нными экологическими требованиями; возникновение т.н. Европейско-Маньчжурской дизъюнкции в области распространения лиственных лесов и связанных с ними водив животных; наконец реликтовые местонахождения определе́нных видов в типичных фаунистических приютах третичного периода: на Мадейре, Сардинии и Корсике, Колхиде и Ленкоранской низменности, а также в некоторых партиях лиственных лесов Азии, принимаемых за остатки Тургайских лесов позволило констатировать, что старейшие партии областей распространения 77 вигов (табл. XIX), то есть 43,50% исследованной фауны, образовались в неогене.

Возможность миграци через пространство Беринга в эпохах оледенения, через пространство Европейско-Маньчжурской дизъюнкции в ээмской межледниковой эпохе, существование Голарктико-Андийской дизъюнкции и некоторые другие признаки областей распространения свидетельствуют, что в 47 случаях исследуемые ареалы частично образовались в четвертичном периоде. Однако только у 20 видов, то есть у 11,30% исследованной фауны, области распространения имеют признаки исключительно четвертичного периода (табл. XX).

В случае 60 видов (33,90%) не удалось установить характерных (возможных связать с определённым историческим периодом) признаков областей распространения (табл. XXI).

6. Соответственно хорошее знакомство развития географической среды и рас-

тительности окрестностей Познани в послеледниковый период, а также экологических требований панцирных клещей, как в отношении микро так и макроклимата, позволило сформулировать гипотезу о развитии фауны панцирных клещей окрестностей Познани в течении последних нескольких тысяч лет (табл. XXII и XXIII). Она касается только видов, обитающих в настоящее время на исследуемом пространстве и кратко представляется следующим образом:

В условиях старейшего дриаса в окрестностях Познани могли обитать лишь те виды панцирных клещей, которые в настоящее время находятся в Арктической области, сносят континентальный климат и могут существовать на местности не покрытой древовидной растительностью, а особенно лесами. Также виды, обитающие среди споровых растений на твёрдом субстрате. 11 видов (6,2%) среди современной фауны соответствует этим условиям. Все они имеют Голарктические области распространения или больше.

В интерстадиале Боллинг поселились на исследуемой местности вероятно виды не приспособившиеся к климату крайне континентальному но обитающие в настоящее время в биоклиматической Арктической зоне. В экологическом отношении это формы открытых пространств или независимые от растительного покрова об различных требованиях влажности. Таких видов в исследуемой фауне 28, то есть 15,82%. Все они имеют очень большие области распрос транения. Эти виды исчезли в Великой Польше или остались в небольшом количестве в старшем дриасе, когда климат значительно ухудшился.

Действительный перелом в развитии фауны панцирных клещей окрестностей Познани наступил вероятно в интерстадиале Аллерод, когда появились условия поселения лесных форм, тырфобионтов, светолюбных форм, связанных со средой нисших растений на твёрдом субстрате, доходящих в настоящее время, на севере, к бореальной биоклиматической зоне. Вместе с формами, которые дошли и поселилис здесь в предыдущие периоды, фауна панцирных клещей насчитывала, вероятно, уже тогда ок. 120 видов то есть 68,93% настоящей фауны. Характерно, что в этот период появилось большое количество видов умеренно Голарктических и палеоарктических, а также некоторое количество европейских видов, за исключением южноевропейских.

Второй регресс в развитии исследуемой фауны произошел в младшем дриассе в связи с повторным ухудшением климата. Вероятно исчезло 37 видов главны образом лесных, которые имели европейские и умеренно Голарктические области распространения. Возвратились они на исследуемое пространство, возможно, уже в предбореальный период.

В Великой Польше, в бореальный период, могли обитать европейские (с исключением западноевропейских) и европейско-маньчжурские мезогигры типичные для лиственных лесов и теплолюбимые виды, юго-восточно-европейского происхождения. Исследуемая фауна тогда, вероятно, обогатились на 30 видов то есть на 17% современной фауны и насчитывала уже около 152 видов, то есть 86% в настоящее время здесь известных.

Остальных 14% видов, главным образом западно и среднеевропейских, появилось, вероятно, в окрестностях Познани в Атлантическом периоде, причём это были преимущественно лесные мезо и полигигры, а также другие формы современно связанные с субокеанским климатом.

В суббореальном и субатлантическом периодах происходили в исследуемой фауне, вероятно, лишь количественные изменения, в связи с уменьшением лесных площадей под влиянием поселений.

Установленные факты и представленные гипотезы интерпретировано и критически продискутировано на фоне современного уровня знаний.

Table I

Holo-European Species

Ser. No. *	Species	Range Diagnosis after MEUSEL et al. (1965)	Ecological Element	Disjunctions	Refuges	Historical Element	Chronoelement
4	*Steganacarus applicatus* (SELLNICK)	m + sm – temp – b, oc_{1-3}, Eur + Mad	df, ph	eur-mad	**Mad**	Alleröd	Neogene
81	*Carabodes marginatus* (MICHAEL)	m – sm – $temp_{mo}$ – b, oc_{1-3}, Eur + NAfr	df, mh	Seur-Nafr	Col, NAfr	Boreal	
152	*Chamobates subglobosus* (OUDEMANS)	m – sm – temp – (b), oc_{1-3}, Eur + NAfr	df, mh	Seur-Nafr	NAfr	Boreal	
78	*Carabodes femoralis* (NICOLET)	m – sm – $temp_{salp}$ – b, oc_{1-3}, Eur	df, mh		**Col, Len**	Boreal	Neogene
73	*Astegistes pilosus* (C. L. KOCH)	sm – temp – b, oc_{1-3}, Eur	op, ph			Alleröd	
83	*Carabodes ornatus* ŠTORKAN	sm – $temp_{salp}$ – b, oc_{1-3}, Eur					
97	*Oppia quadrimaculata* EVANS	sm – temp – b, oc_{1-3}, Eur	df, mh			Boreal	
112	*Cymbaeremaeus cymba* (NICOLET)	sm – $temp_{alp}$ – b, oc_{1-3}, Eur	hs, oh			Alleröd	
114	*Licneremaeus licnophorus* (MICHAEL)	sm – temp – b, oc_{1-3}, Eur	f, omh			Alleröd	
144	*Minunthozetes semirufus* (C. L. KOCH)	sm – $temp_{salp}$ – b, oc_{1-3}, Eur	df, op, mph			Atlantic	
145	*Minunthozetes pseudofusiger* (SCHWEIZER)	sm – temp – b, oc_{1-3}, Eur	n, hs, euh		**Col**	Alleröd	Neogene
153	*Euzetes globulus* (NICOLET)	sm – $temp_{alp}$ – b, oc_{1-3}, Eur	df, pmh		Arm	Atlantic	
157	*Galumna lanceata* (OUDEMANS)	sm – temp – b, oc_{1-3}, Eur	df, op, mh			Boreal	
47	*Damaeus (Damaeus) onustus* C. L. KOCH	sm – $temp_{salp}$ – (b), oc_{1-3}, Eur	df, pmeuh			Atlantic	

* The serial numbers are the same as in the list in the faunictic-ecological parts. The refugial localities that are most likely relict in character are in black type.

Table II

West-European Species

Ser. No.	Species	Range Diagnosis after Meusel et al. (1965)	Ecological Element	Disjunctions	Refuges	Range Boundary (+) and Outmost Point (o) Lying in Poland		Historical Element	Chronoelement
						E	N		
72	*Xenillus permixtus* (André)	m – sm – $temp_{alp}$ – b, oc_{1-2-3}, Eur + Mad + + MAs	df, mh	eur-as, eur-mad	T, II, Mad			Boreal	Neogene
65	*Eueremaeus silvestris* (Forsslund)	m – sm – temp – b, oc_{1-2}, Eur	f, mh		Cors	+		Alleröd	
59	*Cepheus dentatus* (Michael)	sm – $temp_{alp}$ – b, $oc_{1-2-(3)}$, Eur	f, hs			+		Alleröd	
166	*Phauloppia lucorum* (C. L. Koch)	sm – temp – b, $oc_{1-2-(3)}$, Eur	hs, mh			+		Alleröd	
17	*Rhysotritia duplicata* (Grandjean)	sm – temp, $oc_{1-2-(3)}$, Eur	cf, msth		Cors	+	+	Boreal	Neogene
40	*Nanhermannia comitalis* Berlese	sm – temp, oc_{1-2}, Eur	df, op, pst			+	+	Atlantic	
63	*Eremaeus hepaticus* C. L. Koch	sm – temp, oc_{1-2}, Eur	df, op, mh			o+	o+	Atlantic	
88	*Tectocepheus cuspidentatus* Knülle	sm – temp, $oc_{1-2-(3)}$, Eur	df, mph			+	+	Atlantic	
155	*Galumna alata* (Hermann)	sm – temp, $oc_{1-2-(3)}$, Eur	n, ph				o+	Atlantic	
64	*Eueremaeus oblongus* (C. L. Koch)	temp, oc_{1-2}, Eur	hs			o+	o+	Atlantic	Palaeogene
109	*Hydrozetes thienemanni* Strenzke	temp, oc_{1-2}, Eur	ph				+	Atlantic	
111	*Limnozetes rugosus* (Sellnick)	temp, oc_{1-2}, Eur	Sph			+	+	Alleröd	Quaternary
149	*Chamobates schutzi* (Oudemans)	temp, oc_{1-2}, Eur	n				+	Atlantic	

Table III

Central European Species

Ser. No.	Species	Range Diagnosis after Meusel et al. (1965)	Ecological Element	Range Boundary (+) and Outmost Point (o) Lying in Poland				Historical Element	Chronoelement
				W	E	S	N		
50	*Damaeus (Spatiodamaeus) boreus* Bulanova-Zakhvatkina	temp, oc_2, Eur	op, mh	o+		o+		Atlantic	Quaternary
91	*Oppia falcata marginedentata* Strenzke	temp, oc_2, Eur	df, mph		o+	+	+	Atlantic	Holocene
98	*Oppia sigma conjuncta* Strenzke	temp, oc_2, Eur	df, mh		o+	+	+	Atlantic	Holocene
118	*Eupelops hygrophilus* (Knülle)	temp, oc_2, Eur	ph		c+	+	+	Atlantic	Quaternary
165	*Eporibatula gessneri* Willmann	temp, oc_2, Eur		+	+		o+	Atlantic	Quaternary
110	*Limnozetes ciliatus foveolatus* Willmann	temp – b, oc_2, Eur	Sph, ph		o+	+		Alleröd	Quaternary
33	*Trhypochthonius nigricans* Willmann	temp – b, oc_2, Eur	Sph, pst		+			Alleröd	Quaternary
7	*Steganacarus spinosus* (Sellnick)	(sm) – $temp_{salp}$, $oc_{(1)-2-(3)}$, Eur	df, op, pst				+	Atlantic	
105	*Autogneta willmanni* (Dyrdowska)	(sm) – temp, $oc_{(1)-2-(3)}$, Eur	df, mh				+	Boreal	
130	*Ophidiotrichus tecta* (Michael)	(sm) – temp, $oc_{(1)-2-(3)}$, Eur	df, mh		+			Boreal	
62	*Microzetorchestes italicus* (Eyndhoven)	sm – temp – b, $oc_{2-(3)}$, Eur	f, mh	+	o+			Alleröd	
164	*Eporibatula rauschenensis* (Sellnick)	(sm) – temp – (b), $oc_{(1)-2-(3)}$, Eur	hs	+				Alleröd	Palaeogene
85	*Carabodes tenuis* Forsslund	sm – temp – b, $oc_{2-(3)}$, Eur	ph	+	+			Alleröd	

Table IV

South European Species

Ser. No.	Species	Range Diagnosis after Meusel et al. (1965)	Ecological Element	Disjunctions	Range Boundary (+) and Outmost Point (o) Lying in Poland N	Refuges	Historical Element	Chronoelement
11	*Phthiracarus lentulus* (C. L. Koch)	m – sm – $temp_{alp}$, oc_{1-3}, Eur+Mad	df, ph	Seur-mad	+	**Mad**	Atlantic	Neogene
43	*Hermanniella dolosa* Grandjean	m – sm – temp, oc_{1-3}, Eur+Mar	df, mh	Seur-Nafr	o+	Mar	Boreal	
44	*Hermanniella punctulata* Berlese	m – sm – temp, oc_{1-3}, Eur+NAfr	df, mh	Seur-Nafr	o+	Mar, **Col, Len** II	Boreal	Neogene
45	*Hermanniella punctulata septentrionalis* Berlese	m – sm – temp, oc_{1-3}, Eur	df, mh		o+		Boreal	
61	*Zotorchestes micronychus* Berlese	m – sm – temp, oc_{1-3}, Eur+Alg	df, mph	Seur-Nafr	+	Alg, **Len**	Atlantic	Neogene
5	*Steganacarus laevigatus* (C. L. Koch)	sm – $temp_{salp}$, oc_{1-3}, Eur	df, ph		+		Atlantic	
55	*Metabelba pulverosa* Strenzke	sm – temp, oc_{1-3}, Eur	df, mh		o+		Boreal	
128	*Oribatella meridionalis* Berlese	sm – $temp_{alp}$, oc_{1-3}, Eur	(o, omh)?		+		Boreal	Palaeogene
129	*Oribatella reticulata* Berlese	sm – temp, oc_{1-3}, Eur	mh?		o+		Boreal	
117	*Eupelops hirtus* (Berlese)	sm – $temp_{mo}$, $oc_{(1)-2-(3)}$, Eur	df, mh		o+		Boreal	
167	*Dometorina plantivaga* (Berlese)	sm – temp, $oc_{1-2-(3)}$, Eur	hs		+		Boreal	

Table V

East, South-East and North European Species

Ser. No.	Species	Geoelement	Range Diagnosis after MEUSEL et al. (1965)	Ecological Element	Range Boundary (+) and Outmost Point (o) Lying in Poland				Refuges	Historical Element	Chronoelement
					W	E	S	N			
151	*Chamobates voigtsi* (OUDEMANS)	Eeur	(m) – sm – $temp_{salp}$ – b, $oc_{(1)-3}$, Eur	f, mh					**Col, Len**	Alleröd	Neogene
150	*Chamobates spinosus* SELLNICK	Eeur	sm – temp – b, $oc_{(1)-3}$, Eur	n, euh						Alleröd	
52	*Epidamaeus bituberculatus* (KULCZYŃSKI)	Eeur	sm – $temp_{alp}$ – b, oc_{2-3}, Eur	op, mh						Alleröd	
134	*Ceratozetes minimus* SELLNICK	Eeur	temp – (b), oc_{2-3}, Eur	f, mh						Alleröd	
177	*Xylobates variabilis* (RAJSKI)	Eeur	m + temp, $oc_{(1)-3}$, Eur	df, mph	o+		+	+	**Len**	Atlantic	Neogene
163	*Zygoribatula propinquus* (OUDEMANS)	SEeur	m – (sm) – (temp), $oc_{(1-3)}$ – k_1, Eur	op, omh				+		Boreal	
66	*Amerus polonicus* KULCZYŃSKI	SEeur	m – sm – temp, oc_{2-3}, Eur	df, mh	o+			o+	**Col, Len**	Boreal	Neogene
92	*Oppia furcata* (WILLMANN)	SEeur	sm – temp, oc_{2-3}, Eur	op, euh				+		Boreal	
143	*Punctoribates sellnicki* (WILLMANN)	SEeur	sm – (temp) – (b), $oc_{(1)-3}$, Eur	op, Sph, euh						Alleröd	
14	*Phthiracarus tardus* FORSSLUND	Neur	temp – b, oc_2, Eur	cf, mpeuh	+	+	o+			Alleröd	Quaternary
84	*Carabodes subarcticus* TRÄGÅRDH	Neur	(sm) – (temp) – b – – arct, oc_{2-3}, Eur	cf, op, euh						Bölling	

Table VI

European-West Siberian Species

Ser. No.	Species	Range Diagnosis after Meusel et al. (1965)	Ecological Element	Disjunctions	Refuges	Historical Element	Chronoelement
139	*Trichoribates incisellus* (Kramer)	(m) – sm – $temp_{alp}$ – b, oc_{1-3} – (k_1), Eur + WSib	op, mph	eur-as		Alleröd	
121	*Peloptulus phaenotus* (C. L. Koch)	(m) – sm – $temp_{salp}$ – b, oc_{1-3} – (k_1), Eur + Mong	op, pmh	eur-as		Alleröd	
119	*Eupelops occultus* (C. L. Koch)	m – sm – $temp_{alp}$ – b, oc_{1-3}, Eur + WSib + + Mong	op, mph	eur-as	**Len**	Alleröd	Neogene
3	*Tropacarus carinatus* (C. L. Koch)	m – sm – temp – b, oc_{1-3}, Eur + WSib + NAfr	cf, oh	eur-as, Seur-Nafr	Len, Col, Alg	Alleröd	
69	*Liacarus coracinus* (C. L. Koch)	m – sm – $temp_{alp}$ – b, oc_{1-3}, Eur + WSib + + NAfr	f, op, mh	eur-as, Seur-Nafr	Len, II, NAfr	Alleröd	
115	*Eupelops acromios* (Hermann)	m – sm – $temp_{niv}$ – b, oc_{1-3}, Eur + WSib + + NAfr	hs, oh	eur-as, Seur-Nafr	Alg, II	Alleröd	Palaeogene
79	*Carabodes femoralis regusior* Berlese	m – sm – temp – b, oc_{1-3}, Eur + WSib + MAs	f, mh	eur-as	**Len, T**	Alleröd	Neogene
138	*Trichoribates trimaculatus* (C. L. Koch)	sm – $temp_{niv}$ – b – arct, oc_{1-3}, Eur + Mong	op, hs	eur-as		Bölling	
113	*Micreromus brevipes* (Michael)	sm – temp – b, oc_{1-3}, Eur + Mong	hs, oh	eur-as		Alleröd	
75	*Hafenrefferia gilvipes* (C. L. Koch)	sm – temp – b, oc_{1-3}, Eur + WSib	f, mh	eur-as		Alleröd	
89	*Oppia bicarinata* (Paoli)	sm – $temp_{salp}$ – b, oc_{1-3}, Eur + WSib	f, mh	eur-as	**Col**	Alleröd	Neogene
90	*Oppia fallax obsoleta* (Paoli)	sm – $temp_{mo}$ – b, oc_{1-3}, Eur + WSib	n	eur-as		Alleröd	
107	*Oribella pectinata* (Michael)	sm – temp – b, oc_{1-3}, Eur + WSib	mh	eur-as		Alleröd	

108	*Oribella paolii* (OUDEMANS)	sm – $temp_{alp}$ – b, oc_{1-3}, Eur + WSib	op, mh	eur-as		Alleröd	
116	*Eupelops duplex* (BERLESE)	sm – $temp_{alp}$ – b, oc_{1-3}, Eur + WSib	f, mh	eur-as		Alleröd	
135	*Ceratozetes sellnicki* RAJSKI	(sm) – temp – b, oc_{2-3}, Eur + WSib + MAs	n, mh	eur-as	T	Alleröd	Neogene
120	*Eupelops tardus* (C. L. KOCH)	sm – temp, $oc_{(1-)3}$, Eur + + WSib	op, mh	eur-as		Boreal	
94	*Oppia neerlandica* (OUDEMANS)	sm – temp, oc_{1-3}, Eur + + Mong	ph	eur-as		Atlantic	
49	*Damaeus (H.) riparius* NICOLET	sm – $temp_{alp}$, oc_{1-3}, Eur + + WSib	df, mh	eur-as		Boreal	
53	*Epidamaeus kamaensis* (SELLNICK)	temp – (b), oc_{2-3}, Eur + + WSib	n, mh	eur-as		Alleröd	
104	*Autogneta tragardhi* FORSSLUND	(temp) – b, oc_{1-3}, Eur + + WSib	cf, mh	eur-as		Alleröd	
51	*Damaeus (S.) subverticillipes* BULANOVA-ZAKHVATKINA	temp, oc_{2-3}, Eur + WSib	f, mh	eur-as		Boreal	

Table VII

European-Manchurian, European-Siberian and European-Middle Asiatic Species

Ser. No.	Species	Geoelement	Range Diagnosis after Meusel et al. (1965)	Ecological Element	Disjunctions	Refuges	Historical Element	Chrono-element
48	*Damaeus (P.) clavipes* (Hermann)	eur-manch	$m-sm-temp_{alp}-b$, oc_{1-3}, Eur+EAs+NAfr	f, mh	**eur-manch**, Seur-Nafr	EAs, II, NAfr	Alleröd	Quaternary
71	*Xenillus clypeator* Robineau-Desvoidy	eur-manch	$m_{smo}-sm-temp_{salp}-b$, oc_{1-3}, Eur+MAs+ +EAs+NAfr	df, mh	**eur-manch**, Seur-Nafr	T, EAs, II, NAfr, Mad, Col, Len	Boreal	Palaeogene
60	*Gustavia fusifer* (C. L. Koch)	eur-manch	$m-sm-temp_{alp}-b$, oc_{1-3}, Eur+WSib+EAs	f, op, ph	**eur-manch**, eur-mad	EAs, II, Mad, Col, Len	Alleröd	Neogene
28	*Heminothrus targionii* (Berlese)	eur-manch	$sm-temp_{mo}-b$, oc_{1-3}, Eur+EAs	df, msth	**eur-manch**	EAs	Boreal	Neogene
175	*Xylobates badensis* (Sellnick)	eur-manch	$sm-temp_{salp}-b$, oc_{1-3}, Eur+EAs	op, hs, oh	**eur-manch**	EAs	Alleröd	Quaternary
148	*Chamobates pusillus* (Berlese)	eur-manch	$sm-temp_{alp}$, oc_{1-3}, Eur+EAs	f, mh	**eur-manch**	EAs	Boreal	Neogene
74	*Cultroribula falcata* Evans	eur-manch	temp, oc_{1-3}, Eur+WSib+ +EAs	df, mh	**eur-manch**	EAs	Boreal	Neogene
20	*Nothrus palustris* C. L. Koch	eur-sib	$sm-temp_{alp}-b$, oc_1-k_1, Eur+WSib+ESib	n, pmeuh	eur-as	ESib, Kur, Col	Alleröd	
56	*Porobelba spinosa* (Sellnick)	eur-sib	$sm-temp_{alp}-b$, oc_1-k_1, Eur+ESib	f, omh	eur-as	ESib	Alleröd	
142	*Punctoribates hexagonus* Berlese	eur-mas	$m-sm-temp-b$, oc_1-k_1, Eur+MAs	op, Sph			Alleröd	

Table VIII

Temperate-Holo-Holarctic and Alpine Temperate-Holarctic (No. 137) Species

Ser. No.	Species	Range Diagnosis after Meusel et al. (1965)	Ecological Element	Disjunctions	Refuges	Historical Element	Chronoelement
103	*Autogneta longilamellata* (Michael)	$m-sm-temp_{mo}-b$, oc_1-k_1, Eur+As+NAm+NAfr	f, mh	**Npac**, eur-as, Seur-Nafr	EAs	Alleröd	Palaeogene
46	*Gymnodamaeus bicostatus* (C. L. Koch)	$m-sm-temp_{alp}-b$, oc_{1-3}, Eur−As+NAm+NAfr	f, op, mh	**Eas-Nam, eur-manch**, Natl, Seur-Nafr	EAm	Alleröd	Neogene
13	*Phthiracarus piger* (Scopoli)	$m-sm-temp_{salp}-b$, oc_{1-3}, Eur+WAs+EAm+NAfr+Al	f, mh	**Natl**, eur-as, Seur-Nafr	EAm	Alleröd	Neogene
171	*Scheloribates latipes* (C. L. Koch)	$m-sm-temp_{alp}-b$, oc_{1-3}, Eur−As+EAm	op, cf, mph	**eur-manch, Eas-Nam**, Natl	EAs, EAm	Alleröd	Neogene
141	*Punctoribates punctum* (C. L. Koch)	$m-sm-temp_{alp}-b$, oc_1-k_1, Eur−As+EAm	f, op, mh	**Eas-Nam**, Natl	EAs, EAm, T	Alleröd	Neogene
99	*Oppia subpectinata* (Oudemans)	$m-sm-temp_{salp}-b$, oc_1-k_1, Eur−As+EAm	Sph, op, ph	**Eas-Nam**, Natl	EAm, Mad, T	Alleröd	Neogene
93	*Oppia minus* (Paoli)	$m-sm-temp-b$, oc_1-k_1, Eur+MAs+Am	f, mph	eur-as	Len, Col, T	Alleröd	Palaeogene
159	*Pilogalumna tenuiclava* (Berlese)	$m+sm-temp_{alp}-b$, oc_{1-3}, Eur+MAs+EAm+Al	Sph, ph	eur-as, Natl	EAm, **Col**	Alleröd	Neogene
10	*Phthiracarus italicus* (Oudemans)	$m-sm-temp-b$, oc_{1-3}, Eur+WAs+EAm+NAfr	cf, mpeuh	**Natl**, Seur-Nafr	**Len**, EAm	Alleröd	Neogene
58	*Cepheus cepheiformis* (Nicolet)	$sm-temp_{salp}-b$, oc_{1-3}, Eur++EAs+WAm	f, ph	**eur-manch, Npac**	WAm, EAs	Alleröd	Neogene
41	*Nanhermannia coronata* Berlese	$sm-temp_{mo}-b$, oc_{1-3}, Eur++EAs+EAm+WAm	Sph, ph	**eur-manch, Npac**, Natl, Nam	WAm, EAm, EAs	Alleröd	Neogene
57	*Cepheus latus* C. L. Koch	$sm-temp_{salp}-b$, oc_{1-3}, Eur++EAs+EAm	f, mph	**eur-manch, EAs-Nam**, Natl	EAs, EAm	Alleröd	Palaeogene
15	*Euphthiracarus cribrarius* (Berlese)	$(sm)-temp-b$, oc_{1-3}, Eur++WAs+EAm	f, mpeuh	**Natl**, eur-as	EAm	Alleröd	Neogene
136	*Fuscozetes fuscipes* (C. L. Koch)	$sm-temp_{alp}-b$, oc_{1-3}, Eur++WAs+EAm	f, op, mph	**Natl**, eur-as	EAm	Alleröd	Neogene
18	*Microtritia minima* (Berlese)	$sm-temp$, $oc_{1-(3)}$, Eur+WAs++EAm	f, mh	**Natl**, eur-as	EAm	Boreal	Neogene
137	*Fuscozetes setosus* (C. L. Koch)	$sm-temp_{niv}$, oc_{1-3}, Eur++WAs+EAm	Sph, ph	**Natl**	EAm		Neogene

Table IX

Western Temperate-Holarctic Species

Ser. No.	Species	Range Diagnosis after MEUSEL et al. (1965)	Ecological Element	Disjunctions	Refuges	Historical Element	Chronoelement
6	*Steganacarus magnus* (NICOLET)	m – sm – temp – b, $oc_{1-(3)}$, Eur+EAm	df, mpeuh	**Natl**	**Len, Col,** EAm	Atlantic	Neogene
70	*Adoristes ovatus* (C. L. KOCH)	m – sm – $temp_{salp}$ – b, oc_{1-3}, Eur+EAm	cf, moh	**Natl**	**Len,** EAm	Alleröd	Neogene
76	*Carabodes coriaceus* (C. L. KOCH)	m – sm – temp – b, oc_{1-3}, Eur+NAfr+EAm	f, mh	**Natl,** Seur-Nafr	EAm, Alg, II	Alleröd	Palaeogene
127	*Oribatella calcarata* (C. L. KOCH)	m – sm – $temp_{alp}$ – b, oc_{1-3}, Eur+NAfr+Am	f, mh	**Natl,** Seur-Nafr	NAfr	Alleröd	Neogene
160	*Acrogalumna longipluma* (BERLESE)	m – sm – $temp_{alp}$ – b, oc_{1-3}, Eur+Am+Mad	f, mh	**Natl?** eur-mad	Mad	Alleröd	Neogene
9	*Phthiracarus globosus* (C. L. KOCH)	m – sm – $temp_{alp}$ – b, oc_{1-3}, Eur+Mad+EAm	f, pmeuh	**Natl,** eur-mad	EAm, Len, Col, II, Mad	Alleröd	Neogene
147	*Chamobates borealis* (TRÄGÅRDH)	m + sm – $temp_{salp}$ – b, oc_{1-3}, Eur+Mad+Al	f, moh	**Npac?, eur-mad**	**Mad**	Alleröd	Neogene
12	*Phthiracarus ligneus* WILLMANN	sm – temp – b, oc_{1-3}, Eur+Al	f, mh	Npac?	**Col**	Alleröd	Neogene
39	*Nanhermannia nanus* (NICOLET)	sm – $temp_{alp}$ – b, oc_{1-3}, Eur+EAm+WAm	n, mph	**Natl,** Nam	**Col,** EAm, WAm	Alleröd	Neogene
37	*Trimalaconothrus glaber* (MICHAEL)	sm – $temp_{alp}$ – b, oc_{1-3}, Eur+EAm	f, op, ph	**Natl**	EAm	Alleröd	Neogene
54	*Metabelba papillipes* (NICOLET)	sm – temp – (b), oc_{1-3}, Eur+EAm	n, mh	**Natl**	EAm	Boreal	Neogene
82	*Carabodes minusculus* BERLESE	sm – $temp_{alp}$ – b, oc_{1-3}, Eur+EAm	n, mh	**Natl**	EAm	Alleröd	Neogene
140	*Trichoribates novus* (SELLNICK)	sm – $temp_{alp}$ – b, oc_{1-3}, Eur+EAm	op, mh	**Natl**	EAm	Alleröd	Neogene
170	*Liebstadia humerata* SELLNICK	sm – $temp_{alp}$ – b, oc_{1-3}, Eur+EAm	mh	**Natl**	EAm	Alleröd	Neogene

125	*Parachipteria bella* (SELLNICK)	sm – temp – b, oc_{2-3}, Eur + EAm	mh	**Natl**	EAm	Alleröd	Neogene
77	*Carabodes areolatus* BERLESE	(sm) – ($temp_{alp}$) – b, oc_{1-3}, Eur + EAm	f, oh	**Natl**	EAm	Alleröd	Neogene
35	*Malaconothrus gracilis* VAN DER HAMMEN	temp – b, oc_{1-2}, Eur + EAm	op, pmh	**Natl**	EAm	Alleröd	Neogene
42	*Nanhermannia elegentula* BERLESE	sm – temp, oc_{2-3}, Eur + + EAm + WAm	f, mh	**Natl**, Nam	EAm, WAm	Boreal	Neogene
133	*Ceratozetes mediocris* BERLESE	m – sm – $temp_{mo}$, oc_{1-3}, Eur + Mad + EAm	op, mph	**Natl**, eur-mad	EAm, **Mad**	Atlantic	Neogene

Table X

Holo-Holarctic Species

Ser. No.	Species	Range Diagnosis after MEUSEL et al. (1965)	Ecological Element	Disjunctions	Refuges	Historical Element	Chronoelement
161	*Oribatula tibialis* (NICOLET)	$m-sm-temp_{alp}-b-arct, oc_1-k_1, Eur-As+EAm++NAm+Gr$	f, op, mh	Natl, **Npac**	Al, EAm, Sib, Col, Len	Oldest Dryas	Quaternary
162	*Zygoribatula exilis* (NICOLET)	$m-sm-temp_{alp}-b-arct, oc_1-k_1, Eur-As+EAm+NAm+Gr$	hs, oh	Natl, **Npac**	Al, EAm, EAs, Sib	Oldest Dryas	Quaternary
19	*Eulohmannia ribagai* BERLESE	$(m)-sm-temp_{alp}-b-arct, oc_1-k_1, Eur+WSib++EAs+NAm$	f, mph	Natl, **Npac?**, eur-as	Al, EAs	Oldest Dryas	Quaternary
8	*Steganacarus striculus* (C. L. KOCH)	$m+sm-temp_{alp}-b+arct, oc_{1-3}, Eur+WSib+EAs++EAm+NAm+Gr$	n, peuh	**eur-manch**, Natl	EAs, EAm, **Len**	Bölling	Neogene
32	*Trhypochthonius tectorum* (BERLESE)	$m_{alp}+sm-temp-b+arct, oc_{1-3}, Eur+NAs+Him_{alp}++EAs+NAm+Gr$	op, hs, oh	**eur-manch**	EAs, **T**	Bölling	Palaeogene
27	*Camisia spinifer* (C. L. KOCH)	$m-sm-temp_{alp}-b+arct, oc_{1-3}, Eur+EAs+EAm++NAm+Gr+NAfr$	cf, oh	**eur-manch**, Natl, Seur-Nafr, **Npac?**	Al, EAs, EAm, Alg	Bölling	Quaternary
122	*Achipteria coleoptrata* (L.)	$m-sm-temp_{alp}-b-arct, oc_{1-3}, Eur+WSib+EAm++NAm+Gr$	n, mh	**Natl**, eur-manch	II, EAm	Bölling	Neogene
101	*Oppia unicarinata* (PAOLI)	$m-sm-temp_{alp}-b-arct, oc_{1-3}, Eur+WSib+EAm++Gr$	f, moh	**Natl**, eur-as	EAm	Bölling	Neogene
96	*Oppia ornata* (OUDEMANS)	$m-sm-temp_{alp}-b-arct, oc_{1-3}, Eur+WSib+Gr$	f, mph	**Natl**, eur-as	Col, Len	Bölling	Neogene
169	*Liebstadia similis* (MICHAEL)	$m+sm-temp_{alp}-b-arct, oc_{1-3}, Eur+WSib+MAs++NAm+Gr$	op, mh	**Npac**, eur-as	Al, **T**	Bölling	Palaeogene

1	*Hypochthonius rufulus* C. L. KOCH	sm – $temp_{salp}$ – b – (arct), oc_{1-3}, Eur+WSib+EAs+ +EAm+NAm	n, pmeuh	**eur-manch, Npac?** Natl	Al, EAm, EAs	Bölling	Neogene
22	*Nothrus pratensis* SELLNICK	sm – $temp_{salp}$ – b – arct, oc_{1-3}, Eur+EAs+EAm+NAm	Sph, ph	**eur-manch, Npac,** Natl	Al, EAm, EAs	Bölling	Neogene
25	*Camisia biurus* (C. L. KOCH)	sm – $temp_{alp}$ – b – arct, oc_{1-3}, Eur+WSib+EAs+NAm	f, hs	**eur-manch, Npac**	Al, EAs	Bölling	Neogene
30	*Heminothrus paolianus longisetosus* WILLMANN	(sm) – temp – b – arct, oc_{1-3}, Eur+WSib+EAs+NAm+ +Gr	cf, mh	**eur-manch, Npac**	Al, EAs	Bölling	Neogene
106	*Banksinoma lanceolata* (MICHAEL)	sm – temp – b – arct, oc_{1-3}, Eur+WSib+NAm	n, pmh	eur-as, **Npac?**	Al	Bölling	Quaternary
131	*Tegoribates latirostris* (C. L. KOCH)	sm – temp – b – arct, oc_{1-3}, Eur+WSib+NAm	op, ph	eur-as, **Npac?**	Al	Bölling	Quaternary
154	*Neoribates aurantiacus* (OUDEMANS)	sm – $temp_{alp}$ – b – arct, oc_{1-3}, Eur+WSib+NAm	f, mh	eur-as, **Npac?**	Al	Bölling	Quaternary
100	*Oppia translamellata* (WILLMANN)	temp – b – arct, oc_{1-3}, Eur+ +WSib+NAm+Gr	f, op, ph	**Npac?**	Al	Bölling	Quaternary

Table XI

Western Holarctic and Alpine Holarctic (No. 26) Species

Ser. No.	Species	Range Diagnosis after MEUSEL et al. (1965)	Ecological Element	Disjunctions	Refuges	Historical Element	Chronoelement
123	*Parachipteria punctata* (NICOLET)	m – sm – $temp_{alp}$ – b – arct, oc_{1-3}, Eur+Mad+EAm++Gr	op, pmh	Natl, eur-mad	EAm, **Mad, Col, Len**	Bölling	Neogene
146	*Chamobates cuspidatus* (MICHAEL)	m – sm – $temp_{salp}$ – b – arct, oc_{1-3}, Eur+NAfr+EAm++Gr	f, op, pmh	Natl, Seur-Nafr	EAm, NAfr, Col	Bölling	Palaeogene
124	*Parachipteria willmanni* VAN DER HAMMEN	m – sm – $temp_{alp}$ – b – arct, oc_1 – k_1, Eur+Mad+EAm++Gr	op, pmh	**Natl**, eur-mad	EAm, Mad	Oldest Dryas	Neogene
80	*Carabodes labyrinthicus* (MICHAEL)	m – sm – $temp_{alp}$ – b – arct, oc_1 – k_1, Eur+NAm+Gr++Al	f, mh	**Npac?**	Al	Oldest Dryas	Palaeogene
86	*Tectocepheus velatus* (MICHAEL)	sm – temp – b – arct, oc_{1-3}, Eur+Gr	cf, meuh	**Natl**		Bölling	Neogene
29	*Heminothrus thori* (BERLESE)	sm – $temp_{alp}$ – b – arct, oc_{1-3}, Eur+NAm+Gr	op, ph	**Natl**		Bölling	Neogene
174	*Peloribates pilosus* HAMMER	sm+temp+arct, oc_{1-2}, Eur+EAm+NAm+EGr	op	**Natl**	EAm	Bölling	Neogene
126	*Anachipteria latitecta* (BERLESE)	(sm) – (temp) – (b) – arct, oc_{1-2}, Eur+EAm+NAm	f, ph	**Natl**	EAm	Bölling	Neogene
38	*Trimalaconothrus foveolatus* WILLMANN	temp – b – arct, oc_{1-2}, Eur++Gr	Sph, pst	**Natl**		Bölling	Neogene
26	*Camisia horrida* (HERMANN)	m – sm – $temp_{niv}$ – b – arct, oc_1 – k_1, Eur – As+EAm++NAm+Gr+NAfr	hs, euh	Natl, Seur-Nafr, **Npac**	Al, EAm, Sib, Mar	Oldest Dryas	Palaeogene

Subbipolar and Holarctic-

Ser. No.	Species	Range Diagnosis after MEUSEL et al. (1965)
132	*Ceratozetes gracilis* (MICHAEL)	a + m – sm – $temp_{salp}$ – b, oc_{1-3}, Eur + EAs + EAm + NAm + SAm
156	*Galumna elimata* (C. L. KOCH)	a + (m) – sm – $temp_{alp}$ – b, oc_1 – k_1, SWAs + Eur + NAfr + Mad + + EAm + Cap
158	*Pergalumna nervosa* (BERLESE)	a + sm – temp – b, oc_{1-3}, Eur – As + + EAm + Cap
23	*Nothrus silvestris* NICOLET	ast + bst – m – sm – $temp_{salp}$ – b – – arct, oc_1 – k_1, Eur – As + + NAfr + EAm + NZeal
102	*Quadroppia quadricarinata* (MICHAEL)	bst * + m – sm – $temp_{alp}$ – b – arct, oc_{1-3}, Eur + WSib + SEAs + + EAm + NAm + Gr
68	*Ceratoppia bipilis* (HERMANN)	bst * + m – sm – $temp_{alp}$ – b – arct, oc_1 – k_1, Eur – As + NAfr + + Mad + EAm + Gr
16	*Rhysotritia ardua* (C. L. KOCH)	ast + m – sm – $temp_{salp}$ – b – arct, oc_{1-3}, Eur + WSib + MAs + + EAs + Nafr + EAm + NAm + + Pol
21	*Nothrus anauniensis* CANESTRINI et FANZAGO	ast + m – sm – temp – b – arct, oc_{1-3}, Eur + WSib + EAs + + EAm + NAm + Gr + NZeal
2	*Eniochthonius minutissimus* (BERLESE)	ast + sm – temp – b – (arct), $oc_{1-(3)}$, Eur + WSib + EAs + EAm + + (NAm) + SAm + NZeal
173	*Scheloribates pallidulus* (C. L. KOCH)	ast + sm – $temp_{alp}$ – b + arct, oc_{1-3}, Eur + WSib + EAm + + NAm + Gr + SAm

* Author's unpublished materials from North Vietnam.

Table XII

Subtropical Species

Ecological Element	Disjunctions	Refuges	Historical Element	Chronoelement
f, op, pmh	**Natl, eur-manch, N-SAm, Npac?**	EAs, EAm, Al, II	Alleröd	Neogene
op, mph	**Natl**, Seur – Nafr, afr	EAm, Mad, Col, **NAfr**	Alleröd	Neogene
n, pmh	**Natl**, eur – cap	EAm	Alleröd	Neogene
f, mh	Natl, Seur – Nafr	ESib, EAm, Col, Mex, NAfr	Oldest Dryas	Neogene
f, mph	Natl, **eur-manch, Npac?**	EAs, EAm, **Len**, Al	Bölling	Palaeogene
n, mph	Natl, Seur – Nafr, **Npac?**	EAs, EAm, Mad, II, Sib, Al	Oldest Dryas	Palaeogene
n, mpeuh	Natl, **eur-manch**, Npac?, Seur – Nafr	EAs, EAm, Al, II, Pol, T	Bölling	Neogene
op, msth	Natl, **eur-manch, Npac**	EAs, EAm, Col, Len, Al	Bölling	Palaeogene
n, mpeuh	Natl, **eur-manch, Spac** N – Sam	EAs, EAm, Col	Alleröd	Palaeogene
n, pmh	Natl, eur – as, **Npac, N-Sam**	EAs, EAm, Al	Bölling	Quaternary

Ser. No.	Species	Geoelement	Range Diagnosis after MEUSEL et al. (1965)
172	*Scheloribates laevigatus* (C. L. KOCH)	temp-hol-trop	ast + $trop_{alp}$ + m – sm – $temp_{alp}$ – b, oc_1 – k_1, Eur – As + EAm
24	*Camisia segnis* (HERMANN)	temp-hol-trop	$trop_{alp}$ + m – sm – $temp_{salp}$ – b, oc_{1-3}, Eur + NAfr + EAm + + NAm + SAm
176	*Xylobates capucinus* (BERLESE)	temp-hol-trop	$trop_{mo\text{-}salp}$ + m – sm – temp – b, oc_{1-3}, Eur + WSib + MAs + + EAm + SAm
87	*Tectocepheus serakensis* TRÄGÅRDH	temp-hol-trop	trop + sm – $temp_{salp}$ – b – (arct), oc_1 – k_1, Eur + Gr + Haw
95	*Oppia nova* (OUDEMANS)	semi-cosm	ant + a + trop + bst * + m – sm – – $temp_{alp}$ – b – arct, oc_1 – k_1, Eur + MAs + WSib + EAs + Mad + + EAm + NAm + Gr + SAm
31	*Platynothrus peltifer* (C. L. KOCH)	semi-cosm	a + ast + m – sm – $temp_{alp}$ – b – – arct, oc_1 – k_1, Eur – As + + EAm + NAm + Gr + NZeal
34	*Trhypochthoniellus excavatus* (WILLMANN)	semi-cosm	a + ast + trop + sm – temp – b, oc_{1-2-3}, Eur + SAm + NZeal
36	*Trimalaconothrus novus* (SELLNICK)	semi-cosm	a – ast + sm – temp – b – arct, oc_{1-3}, Eur + NAm + Gr + SAm + NZeal
168	*Hemileius initialis* (BERLESE)	semi-cosm	a + trop + sm – $temp_{alp}$ – b, oc_{1-3}, Eur + EAs + SAm
67	*Fosseremus quadripertitus* GRANDJEAN	semi-cosm	a – ast + m – sm – temp – b, oc_{1-3}, Eur + MAs + NAfr + WAm + NZeal + EAs

* Author's unpublished materials from North Vietnam.

Table XIII

Semi-Cosmopolitan Species

Ecological Element	Disjunctions	Refuges	Historical Element	Chrono-element
op, mpeuh	Natl, **Npac**, Seur-Nafr	EAS, EAm, Col, Len, II, Cors	Alleröd	Neogene
hs, euh	**Natl, Npac?, N-Sam,** Seur-Nafr	EAm, NAfr, Al	Alleröd	Neogene
n, euh	**Natl, N-Sam,** eur-as	EAm, Col, Len, **T**	Alleröd	Neogene
n, mh			Oldest Dryas	
f, mph	**Natl, N-Sam,** eur-as	EAs, EAm, Mad, Col, Len, T	Oldest Dryas	Neogene
n, mph	**Natl, Npac**	EAs, EAm, Col, Len, Al, Sib	Oldest Dryas	Quaternary
Sph, ph	**Spac**		Alleröd	Palaeogene
Sph, pst	**Npac? Spac,** N-Sam	Al	Alleröd	Palaeogene
op, f, mh	**eur-manch**	EAs	Alleröd	Neogene
n, pmh	**eur-manch, Npac,** Seur-Nafr	EAs, Len, NAfr, WAm, T	Alleröd	Neogene

Table XIV

Percentage Share of Species with Various Types of Ranges in Moss Mite Fauna of Poznań Region

Species	%	%
holo-European	7·81	
West European	7·35	
Central European	7·35	
South European	6·22	
East European	2·82	
South-East European	2·26	
North European	1·13	
European s. l.		34·94
European-West Siberian	12·43	
European-Manchurian	3·96	
European-Siberian	1·13	
European-Middle Asiatic	0·56	
Palaearctic (total)		18·08
temperate-holo-Holarctic	8·46	
western temperate-Holarctic	10·73	
alpine temperate-Holarctic	0·56	
temperate-Holarctic s. l.		19·70
holo-Holarctic	10·17	
western Holarctic	5·09	
alpine Holarctic	0·56	
Holarctic s. l.		15·82
subbipolar	2·09	
Holarctic-subtropical	3·96	
temperate-Holarctic-tropical	2·26	
semi-cosmopolitan	3·27	
widely distributed (all together)		11·58
total	100·00	100·00

Table XV

Percentage Share of N, S, E, and W Species (in Relation to Poznań in the Fauna under Study, Irrespective of the Kind of Range

species / range	N	S	E	W	SE	alp
eur				7·35		
eur		6·22				
eur			2·82			
eur					2·26	
eur	1·13					
eur-W-sib	0·57	1·69				
eur-man		0·56				
eur-mas					0·56	
temp-hhol		0·56				
temp-hol. W	0·56	1·13				
temp-hol						0·56
hhol	1·13					0·56
W-hol	1·13					
total	4·52	10·16	2·82	7·35	2·82	1·12

Table XVI

Relations between Ecological and Geographical Elements

Geographical Element \ Ecological Element	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	f	f, op	df	df, op	cf	cf, op	f, hs	hs	op, hs	n, hs	Sph	Sph, op	op	n	ncl
eur	1		7					1		1			1		1
W-eur	1		2	2	1		1	2			1			2	1
C-eur	1		4	1				1			2		1		3
S-eur			8					1					1		1
E-eur	2		1										1	1	
ES-eur			1									1	2		
N-eur					1	1									
eur-W-sib			1		2			2	1				5	3	2
eur-manch	6		3						1						
eur-sib	2	1												1	
eur-mas												1			
temp-hol	7	3				1					2	1			
temp-hol, W	8	1	1		2								3	3	2
temp-hol-alp											1				
hol	4	2			2		1	1	1		1		2	4	
W-hol	2	1			1						1		4		
hol-alp								1							
sbip		1											1	1	
hol-sbt	2												1	4	
temp-hol-trop								1					1	2	
semi-cosm	1	1									2			2	
Total of Species	38	10	28	5	9	2	2	10	3	1	10	3	23	23	10
%	21·47	5·65	15·82	2·83	5·08	1·13	1·13	5·65	1·69	0·57	5·65	1·69	12·99	12·99	5·65

Table XVII

Relations between Climatic Types and Geographical Elements

Geographical Element \ Climatic Type	1	2	3	4	5	6	7	8	9
	$oc_{1-2-3}-k_1$	oc_{1-2-3}	$oc_{1-2-(3)}$	$oc_{(1)-2-3}$	$oc_{(1)-2-(3)}$	oc_{1-2}	oc_{2-3}	$oc_{2-(3)}$	oc_2
heur		14							
W-eur		1	5			7			
C-eur					4			2	7
S-eur		9	1		1				
E-eur				3			2		
ES-eur	1			1			2		
N-eur							1		1
eur-W-sib	2	16		1			3		
eur-manch		7							
eur-sib	2								
eur-mas	1								
temp-hhol	4	9	1	1					
temp-hol, W		16	1			1	2		
temp-hol-alp		1							
hhol	3	15							
W-hol	2	4				3			
hol-alp						1			
sbip	1	2							
hol-sbt	2	4	1						
temp-hol-trop	2	2							
semi-cosm	2	4							
Total	22	104	9	5	5	12	10	2	8
%	12·43	69·49				6·78	6·78		4·52

Table XVIII

Relations between Humidity Requirements of Moss Mites and Their Range Sizes

Humidity Requirements / Geographical Element	poly		meso		oligo		eury		ncl	
	No. of Species	%	No. of Species	%	No. of Species	%	No. of Species	%	No. of Species	%
eur	15	34·1	31	31·0	4	30·8	5	62·5	7	58·3
pal	4	9·1	20	20·0	5	38·5	—	—	3	25·0
temp – hol	8	18·1	26	26·0	1	7·7	—	—	—	—
hol	11	25·0	11	11·0	3	23·0	1	12·5	2	16·6
widely distributed	6	13·7	12	12·0	—	—	2	25·0	—	—
Total	44	100·0	100	100·0	13	100·0	8	100·0	12	100·0

Table XIX

Range Fragments Formed in the Neogene

Geographical Element	Disjunctions			Relict Localities				Number of Species Dated	Total Number of Species
	Natl	eur-manch	Eas—Nam	Col, Len	T	Mad	Cors		
1	2	3	4	5	6	7	8	9	10
heur				2		1		3	14
W-eur					1		1	2	13
S-eur				2		1		3	11
E-eur				2				2	5
ES-eur				1				1	4
eur-W-sib				3	2			4	22
eur-manch		5			1			4	5
temp-hhol	5	5	7	2				12	15
temp-hol-alp	1							1	1
temp-hol, W	17			4		2		18	19
hhol	3	7		1	2			9	18
W-hol	6			1		1		7	9
sbip	3	1	1					3	3
hol-sbt	2	4		1	1			2	7
temp-hol-trop	3				1			3	4
semi-cosm	2	2	1		1			3	6
	42	24	9	19	9	5	1	77	

Table XX

Range Fragments Formed in the Quaternary

Geographical Element	Disjunctions			Postglacial Range	Number of Species Dated	Total Number of Species
	Bering	hol — and	eur — manch			
W-eur				1	1	13
C-eur				7	7	13
N-eur				1	1	2
eur-manch			5		2	7
temp-hhol	1					15
temp-hol, W	2					19
hhol	14				7	18
W-hol	1					9
hol-alp	1					1
sbip	1	1				3
hol-sbt	5	1			1	7
temp-hol-trop	1	2				4
semi-cosm	2	1			1	6
	28	5	5	9	20	

Table XXI

Probable Minimum Age of Species in the Moss Mite Fauna Examined

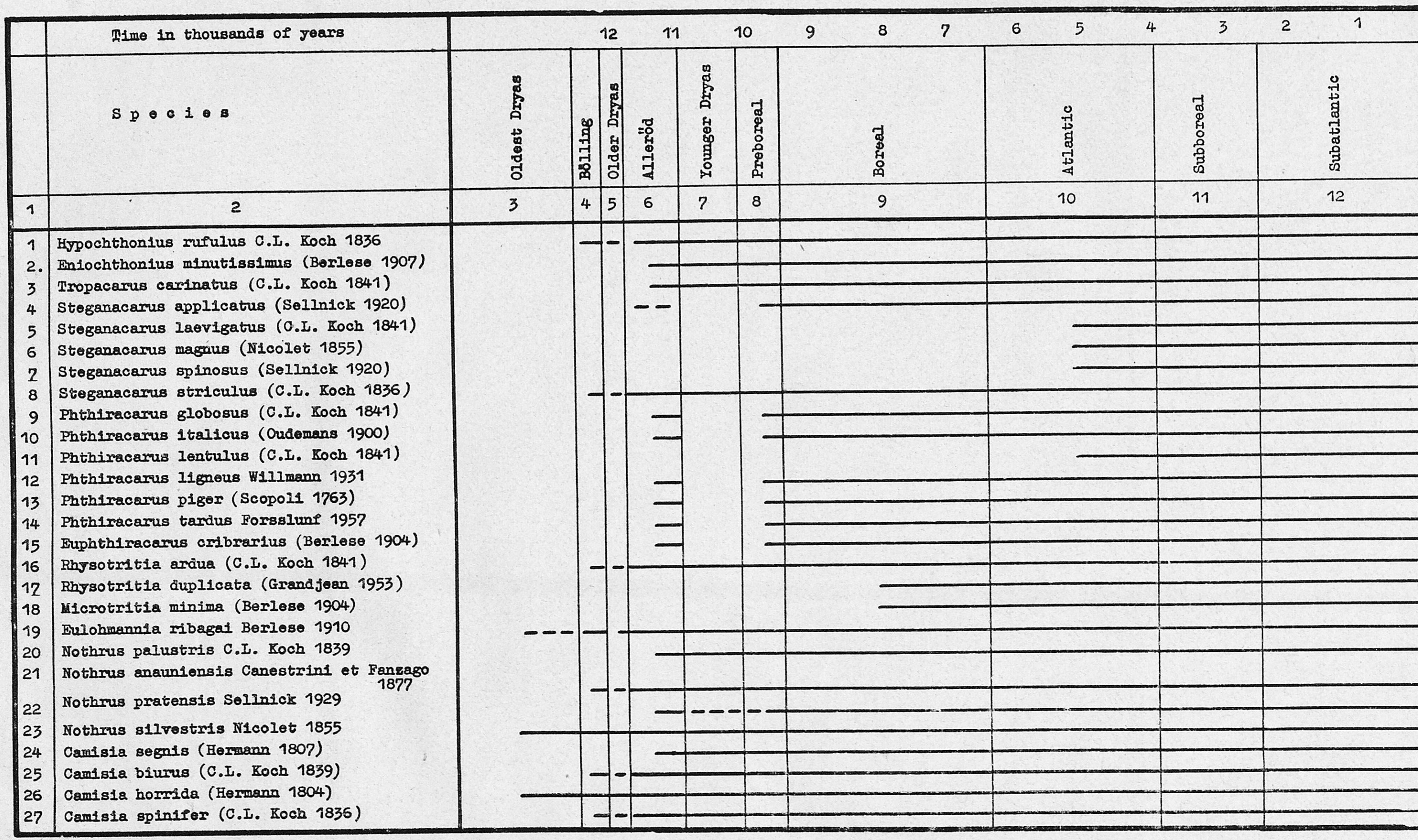
Geographical Element	Palaeogene	Neogene	Quaternary	Non-Dated	Total
heur		3		11	14
W-eur	1	2	1	9	13
C-eur	1		7	5	13
S-eur	1	3		7	11
E-eur		2		3	5
ES-eur		1		3	4
N-eur			1	1	2
eur-W-sib	1	4		17	22
eur-mas				1	1
eur-sib				2	2
eur-manch	1	4	2		7
temp-hhol	3	12			15
temp-hol-alp		1			1
temp-hol-W	1	18			19
hhol	2	9	7		18
hol-alp	1				1
W-hol	2	7			9
sbip		3			3
hol-sbt	4	2	1		7
temp-hol-trop		3		1	4
semi-cosm	2	3	1		6
Total	20	77	20	60	177
%	11·3	43·5	11·3	33·9	100

Chronology of Appearance of Particular Geographical Elements in the Poznań Region in the Late Glacial and Holocene

Period \ Geographical Element	heur	W-eur	C-eur	S-eur	E-eur	SEeur	Neur	eur-W-sib	eur-manch	eur-sib	eur-mas	temp-hhol	temp-hol, W	temp-hol-alp	hhol	W-hol	hol-alp	sbip	hol-sbt	temp-hol-trop	semi-cosm	Total	Percentage	Total of Percentages in particular Periods
Oldest Dryas															3	2	1		2	1	2	11	6·22	6·22
Bölling							1	1							15	7			4			28	15·82	22·04
Older Dryas							−1	−1							−15	−7			−4			−28	−15·82	6·22
Alleröd	5	4	5		4	1	2	18	3	2	1	14	15		15	7		3	5	3	4	111	62·71	68·93
Younger Dryas	−2	−3	−3		−3			−5	−1	−1		−9	−8								−2	−37	−20·89	48·03
Total	3	1	2		1	1	2	13	2	1	1	5	7		18	9	1	3	7	4	4	85	48·03	
Preboreal	2	3	3		3			5	1	1		9	8								2	37	20·89	68·93
Boreal	5	2	2	8		3		3	4			1	2									30	16·95	85·88
Atlantic	3	7	6	3	1			1					2									23	12·99	98·87
Total	13	13	13	11	5	4	2	22	7	2	1	15	19		18	9	1	3	7	4	6	175	98·87	
ncl	1													1								2	1·13	

Table XXIII

History of Species of Moss Mite Fauna in Poznań Region during the Late Glacial and Holocene



1	2	3	4	5	6	7	8	9	10	11	12
28	Heminothrus targionii (Berlese 1885)							—	—	—	—
29	Heminothrus thori (Berlese 1904)		–	–	—	—	—	—	—	—	—
30	Heminothrus paolianus longisetosus Willmann 1925		–	–	—	—	—	—	—	—	—
31	Platynothrus peltifer (C.L. Koch 1839)	—	—	—	—	—	—	—	—	—	—
32	Trhypochthonius toctorum (Berlese 1896)		–	–	—	—	—	—	—	—	—
33	Trhypochthonius nigricans Willmann 1928				—		—	—	—	—	—
34	Trhypochthoniellus excavatus (Willmann 1919)				—		—	—	—	—	—
35	Malaconothrus gracilis van der Hammen 1952				—	—	—	—	—	—	—
36	Trimalaconothrus (T.) novus (Sellnick 1922)				—		—	—	—	—	—
37	Trimalaconothrus (T.) glaber (Michael 1888)				—	—	—	—	—	—	—
38	Trimalaconothrus (T.) foveolatus Willmann 1931		–	–	—	—	—	—	—	—	—
39	Nanhermannia nanus (Nicolet 1855)				—	—	—	—	—	—	—
40	Nanhermannia comitalis Berlese 1913								—	—	—
41	Nanhermannia coronata Berlese 1913				—		—	—	—	—	—
42	Nanhermannia elegantula Berlese 1913							—	—	—	—
43	Hermanniella dolosa Grandjean 1931							—	—	—	—
44	Hermanniella punctulata Berlese 1908							—	—	—	—
45	Hermanniella punctulata septentrionalis Berlese 1910							—	—	—	—
46	Gymnodamaeus bicostatus (C.L. Koch 1836)				—	—	—	—	—	—	—
47	Damaeus (D.) onustus C.L. Koch 1871								—	—	—
48	Damaeus (P.) clavipes (Hermann 1807)				—		—	—	—	—	—
49	Damaeus (H.) riparius Nicolet 1855							—	—	—	—
50	Damaeus (S.) boreus Bulanova-Zakhvatkina 1957								—	—	—
51	Damaeus (S.) subverticillipes Bulanova-Zakhvatkina 1957							—	—	—	—
52	Epidamaeus bituberculatus (Kulczyński 1902)				—	—	—	—	—	—	—
53	Epidamaeus kamaensis (Sellnick 1926)				—	—	—	—	—	—	—
54	Metabelba papillipes (Nicolet 1855)							—	—	—	—
55	Metabelba pulverosa Strenzke 1953							—	—	—	—
56	Porobelba spinosa (Sellnick 1920)				—		—	—	—	—	—
57	Cepheus latus C.L. Koch 1836				—		—	—	—	—	—
58	Cepheus cepheiformis (Nicolet 1855)				—		—	—	—	—	—
59	Cepheus dentatus (Michael 1888)				—		—	—	—	—	—

Table XXIII continued

	Time in thousands of years	12			11		10	9 8 7	6 5 4	3	2 1
	Species	Oldest Dryas	Bölling	Older Dryas	Alleröd	Younger Dryas	Preboreal	Boreal	Atlantic	Subboreal	Subatlantic
1	2	3	4	5	6	7	8	9	10	11	12
60	Gustavia fusifer (C.L. Koch 1841)				—	—	—	—	—	—	—
61	Zetorchestes micronychus (Berlese 1883)								—	—	—
62	Microzetorchestes italicus (Eyndhoven 1942)				—		—	—	—	—	—
63	Euremaeus hepaticus C.L. Koch 1836								—	—	—
64	Eueremaeus oblongus (C.L. Koch 1836)								—	—	—
65	Eueremaeus silvestris (Forsslund 1957)				—		—	—	—	—	—
66	Amerus polonicus Kulczyński 1902							—	—	—	—
67	Fosseremus quadripertitus Grandjean 1965				—	—	—	—	—	—	—
68	Ceratoppia bipilis (Hermann 1804)	—	—	—	—	—	—	—	—	—	—
69	Liacarus coracinus (C.L. Koch 1841)				—	—	—	—	—	—	—
70	Adoristes ovatus (C.L. Koch 1840)				—		—	—	—	—	—
71	Xenillus clypeator Robineau-Desvoidy 1839							—	—	—	—
72	Xenillus permixtus (André 1925)							—	—	—	—
73	Astegistes pilosus (C.L. Koch 1840)				—	—	—	—	—	—	—
74	Cultroribula falcata Evans 1952							—	—	—	—
75	Hafenrefferia gilvipes (C.L. Koch 1839)				—		—	—	—	—	—
76	Carabodes coriaceus C.L. Koch 1836				—		—	—	—	—	—
77	Carabodes areolatus Berlese 1916				—		—	—	—	—	—
78	Carabodes femoralis (Nicolet 1855)							—	—	—	—
79	Carabodes femoralis rugosior Berlese 1916				—		—	—	—	—	—
80	Carabodes labyrinthicus (Michael 1879)	—	—	—	—	—	—	—	—	—	—
81	Carabodes marginatus (Michael 1884)							—	—	—	—
82	Carabodes minusculus Berlese 1923				—	—	—	—	—	—	—
83	Carabodes ornatus Storkan 1925										
84	Carabodes subarcticus Trägårdh 1902		- -	- -	—	—	—	—	—	—	—
85	Carabodes tenuis Forsslund 1953				—	—	—	—	—	—	—
86	Tectocepheus velatus (Michael 1880)		- -	- -	—	—	—	—	—	—	—

1	2	3	4	5	6	7	8	9	10	11	12
87	Tectocepheus sarekensis Trägårdh 1910										
88	Tectocepheus cuspidentatus Knülle 1957										
89	Oppia bicarinata (Paoli 1908)										
90	Oppia fallax obsoleta (Paoli 1908)										
91	Oppia falcata marginedentata Strenzke 1951										
92	Oppia furcata (Willmann 1928)										
93	Oppia minus (Paoli 1908)										
94	Oppia neerlandica (Oudemans 1900)										
95	Oppia nova (Oudemans 1902)										
96	Oppia ornata (Oudemans 1900)										
97	Oppia quadrimaculata Evans 1952										
98	Oppia sigma conjuncta Strenzke 1951										
99	Oppia subpectinata (Oudemans 1900)										
100	Oppia translamellata (Willmann 1923)										
101	Oppia unicarinata (Paoli 1908)										
102	Quadroppia quadricarinata (Michael 1885)										
103	Autogneta longilamellata (Michael 1885)										
104	Autogneta tragardhi Forsslund 1947										
105	Autogneta willmanni (Dyrdowska 1929)										
106	Banksinoma lanceolata (Michael 1888)										
107	Oribella pectinata (Michael 1885)										
108	Oribella paolii (Oudemans 1913)										
109	Hydrozetes thienemanni Strenzke 1943										
110	Limnozetes ciliatus foveolatus Willmann 1939										
111	Limnozetes rugosus (Sellnick 1923)										
112	Cymbaeremaeus cymba (Nicolet 1855)										
113	Micreremus brevipes (Michael 1888)										
114	Licneremaeus licnophorus (Michael 1888)										
115	Eupelops acromios (Hermann 1807)										
116	Eupelops duplex (Berlese 1916)										
117	Eupelops hirtus (Berlese 1916)										
118	Eupelops hygrophilus (Knülle 1954)										
119	Eupelops occultus (C.L. Koch 1836)										
120	Eupelops tardus (C.L. Koch 1836)										

Notice: No 63 should be: Eremaeus

Table XXIII continued

	Time in thousands of years	12			11		10	9 8 7	6 5 4	3	2 1
	Species	Oldest Dryas	Bølling	Older Dryas	Alleröd	Younger Dryas	Preboreal	Boreal	Atlantic	Subboreal	Subatlantic
1	2	3	4	5	6	7	8	9	10	11	12
121	Peloptulus phaenotus (C.L. Koch 1844)				—	—	—	—	—	—	—
122	Achipteria coleoptrata (L.) 1758		–	–	—	—	—	—	—	—	—
123	Parachipteria punctata (Nicolet 1855)		–	–	—	—	—	—	—	—	—
124	Parachipteria willmanni van der Hammen 1952	—	—	—	—	—	—	—	—	—	—
125	Parachipteria belle (Sellnick 1929)				—	—	—	—	—	—	—
126	Anachipteria latitecta (Berlese 1908)		–	–	—	—	—	—	—	—	—
127	Oribatella calcaráta (C.L. Koch 1836)				—		—	—	—	—	—
128	Oribatella meridionalis Berlese 1908							—	—	—	—
129	Oribatella reticulata Berlese 1916							—	—	—	—
130	Ophidiotrichus tecta (Michael 1883)							—	—	—	—
131	Tegoribates latirostris (C.L. Koch 1844)		–	–	—	—	—	—	—	—	—
132	Ceratozetes gracilis (Michael 1844)				—	—	—	—	—	—	—
133	Ceratozetes mediocris Berlese 1908								—	—	—
134	Ceratozetes minimus Sellnick 1929				—		—	—	—	—	—
135	Ceratozetes sellnicki Rajski 1958				—	—	—	—	—	—	—
136	Fuscozetes fuscipes (C.L. Koch 1844)				—	—	—	—	—	—	—
137	Fuscozetes setosus (C.L. Koch 1840)				—	—	—	—	—	—	—
138	Trichoribates trimaculatus (C.L. Koch 1836)		–	–	—	—	—	—	—	—	—
139	Trichoribates incisellus (Kramer 1897)				—	—	—	—	—	—	—
140	Trichoribates novus (Sellnick 1929)				—	—	—	—	—	—	—
141	Punctoribates punctum (C.L. Koch 1839)				—	—	—	—	—	—	—
142	Punctoribates hexagonus Berlese 1908				—	—	—	—	—	—	—
143	Punctoribates sellnicki (Willmann 1928)				—	—	—	—	—	—	—
144	Minumthozetes semirufus (C.L. Koch 1841)								—	—	—
145	Minumthozetes pseudofusiger (Schweizer 1922)				—	—	—	—	—	—	—
146	Chamobates cuspidatus (Michael 1884)		–	–	—	—	—	—	—	—	—

1	2	3	4	5	6	7	8	9	10	11	12
147	Chamobates borealis (Trägårdh 1902)				—		—	—	—	—	—
148	Chamobates pusillus (Berlese 1895)							—	—	—	—
149	Chamobates schutzi (Oudemans 1902)								—	—	—
150	Chamobates spinosus Sellnick 1929				—	—	—	—	—	—	—
151	Chamobates voigtsi (Oudemans 1902)				—	—	—	—	—	—	—
152	Chamobates subglobulus (Oudemans 1900)							—	—	—	—
153	Euzetes globulus (Nicolet 1855)								—	—	—
154	Neoribates aurantiacus (Oudemans 1913)		—	—	—	—	—	—	—	—	—
155	Galumna alata (Hermann 1804)								—	—	—
156	Galumna elimata (C.L. Koch 1841)				—	—	—	—	—	—	—
157	Galumna lanceata (Oudemans 1900)							—	—	—	—
158	Pergalumna nervosa (Berlese 1914)				—	—	—	—	—	—	—
159	Pilogalumna tenuiclava (Berlese 1908)				—		—	—	—	—	—
160	Acrogalumna longipluma (Berlese 1904)				—		—	—	—	—	—
161	Oribatula tibialis (Nicolet 1855)	—	—	—	—	—	—	—	—	—	—
162	Zygoribatula exilis (Nicolet 1855)	—	—	—	—	—	—	—	—	—	—
163	Zygoribatula propinquus (Oudemans 1902)							—	—	—	—
164	Eporibatula rauschenensis (Sellnick 1909)				—	—	—	—	—	—	—
165	Eporibatula gessneri Willmann 1932								—	—	—
166	Phauloppia lucorum (C.L. Koch 1841)				—	—	—	—	—	—	—
167	Dometorina plantivaga (Berlese 1896)							—	—	—	—
168	Hemileius initialis (Berlese 1908)				—	—	—	—	—	—	—
169	Liebstadia similis (Michael 1888)		—	—	—	—	—	—	—	—	—
170	Liebstadia humerata Sellnick 1929				—	—	—	—	—	—	—
171	Scheloribates latipes (C.L. Koch 1844)				—	—	—	—	—	—	—
172	Scheloribates laevigatus (C.L. Koch 1836)				—	—	—	—	—	—	—
173	Scheloribates pallidulus (C.L. Koch 1840)		—	—	—	—	—	—	—	—	—
174	Peloribates pilosus Hammer 1952		—	—	—	—	—	—	—	—	—
175	Xylobates badensis (Sellnick 1929)				—	—	—	—	—	—	—
176	Xylobates capucinus (Berlese 1908)				—	—	—	—	—	—	—
177	Xylobates variabilis (Rajski 1958)								—	—	—

Redaktor zeszytu: dr L. Sych

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